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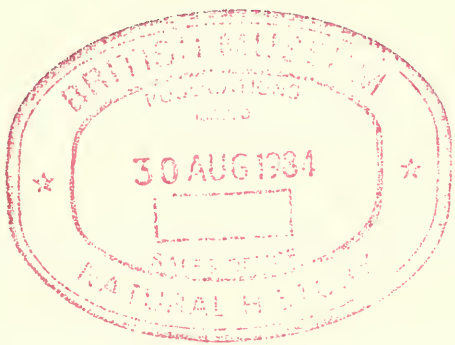

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A review of the Mastacembeloidei, a suborder of synbranchiform teleost fishes Part I: Anatomical descriptions

Robert A. Travers

Zoology series Vol 46 No 1 26 January 1984

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A review of the Mastacembeloidei, a suborder of synbranchiform teleost fishes
Part I: Anatomical descriptions

Robert A. Travers
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[1]This research was carried out in the Department of Zoology, British Museum (Natural History) and was submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy in the Faculty of Science, University of London. The author's present address: Department of Anatomy & Cell Biology, St. Mary's Hospital Medical School, Norfolk Place, London W2 1PG.

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Synopsis

The Mastacembeloidei or spiny eels (comprising the families Mastacembelidae, Chaudhuriidae and Pillaiidae) is a distinctive group of about 70 freshwater species with a tropical and subtropical Oriental and Ethiopian distribution, currently recognised as a suborder of the perciform fishes. The majority of its 70 species have been placed in a single genus, *Mastacembelus*, without regard to their genealogical relationships, and the sub-order as a whole has not been the subject of a detailed taxonomic or anatomical review. A revision of the genera and families within the suborder, and a reconsideration of its interrelationships within the Percomorpha, are the overall objectives of this study.

The present work consists of anatomical descriptions of all available mastacembeloid species. The osteology of *Mastacembelus mastacembelus, Chaudhuria caudata* and *Pillaia indica* is described in detail, and is compared with that in the majority of described species. Myological studies are restricted to the cephalic region (jaw and opercular muscles only), and the arrangement in *Mastacembelus mastacembelus* is described and compared with that found in the other mastacembeloids examined.

Introduction

The Mastacembelidae, or spiny eels, a family of eel-like percomorph fishes is widely distributed in tropical and subtropical regions of Africa, SE. Asia and the Middle East (Ethiopian and Oriental zoogeographic regions). The eel-like appearance of mastacembelids is enhanced by lack of pelvic fins, a long body with numerous vertebrae, a tendency for the dorsal and anal fins to be confluent with the caudal fin, and a narrow, tapered cranium terminating in a pointed rostral appendage. Anterior to the rayed dorsal fin in almost all species is a long series of isolated spines.

The present state of mastacembélid taxonomy is confused. No revision of the entire family has ever been undertaken. Since the first scientific description of this group (Russell, 1756; Gronovius, 1763 & Scopoli, 1777) numerous species have been described, most of which were placed in the genus *Mastacembelus* Scopoli, 1777. Exceptionally, one species, originally described by Bloch (1786, & see Sufi, 1956: 100) was placed in a separate genus, *Macrognathus* Lacépède, 1800 (Bloch's *Ophidium*).

The most recent synoptic review of *Mastacembelus* was published by Boulenger (1912) who recognised 14 Asian, 1 Middle Eastern and 30 African species. Since then, numerous descriptions of new species, particularly from Africa, have appeared in the literature (Table 1), and one was assigned to a new genus (Poll, 1958). However, the validity of this generic distinction was questioned by Roberts & Stewart (1976). Many unidentifiable African specimens lodged in the collections of major national museums including the British Museum (Natural History); Museum of Comparative Zoology, Harvard, and Koninklijk Museum Voor Midden-Afrika, Tervuren, justify the need for a revision of the African mastacembelids.

The state of Oriental mastacembelid taxonomy is little better, although it has been the subject of a more recent revision (Sufi, 1956). Sufi (op. cit.) recognised 15 oriental *Mastacembelus* species and a single *Macrognathus* species on the basis of superficial anatomical and morphometric characters.

Macrognathus remained monotypic until recently (Roberts, 1980). Evidence in support of splitting the single *Macrognathus* species into 3 taxa and expanding this genus to include other species is provided here.

The interrelationships of the mastacembelids with other teleostean fishes have had no less a long and obscure history. Major general classifications treating the Mastacembelidae and their affinities are summarised in Table 2. Their appearance caused the early describers in the latter part of the eighteenth and early nineteenth century to associate them with the true eels (Anguilliformes). By the middle of the nineteenth century Günther (1861) had noticed their many affinities to acanthopterygian fishes and considered them 'acanthopterous eels' distantly related to the Blenniidae. However, it was not until Boulenger (1904) that they were given separate subordinal status, as the Opisthomi, within the Teleostei. Following this, Regan (1912) elevated them to ordinal rank, although he could not trace their affinity to any particular group. Berg (1947: 494) followed Regan (op. cit.) in giving the mastacembelids separate ordinal status (Mastacembeliformes) within the teleosts, but Greenwood, Rosen, Weitzman & Myers (1966) in their phyletic study of teleostean fishes reduced the taxon to subordinal status and included the Mastacembeloidei as one of their 20 suborders in the order Perciformes. This arrangement, apart from slight changes, has remained to the present day.

In addition to the Mastacembelidae, two monotypic families have been included in the suborder Mastacembeloidei. Annandale (1918) erected the family Chaudhuriidae to accommodate a small eel-like fish collected from the Inle Lake, Burma (and recently also collected from Thailand; Roberts, 1980). He considered this small eel-like taxon to be a member of the true eels (Anguilliformes) but was unable to assign it to any known family, partly as a result of its distinct 'fan-shaped' caudal fin (Whitehouse, 1918). Regan (1919), considering the characters described for Chaudhuriidae, showed its affinity to mastacembelids rather than to true eels and placed it in the Mastacembeliformes (his Opisthomi). On the basis of this and new anatomical descriptions, Annandale & Hora (1923) followed his classification as did Mitra & Ghosh (1931) on the basis of the soft anatomy. Berg (1947), however, considered

Table 1 African species assigned to the genus *Mastacembelus* (in chronological order of their description).

Species	Authority	Date
**Mastacembelus cryptacanthus*	Günther	1867
Mastacembelus niger	Sauvage	1878
Mastacembelus marchii	Sauvage	1892
Mastacembelus marmoratus	Perugia	1892
Mastacembelus tanganicae	Günther	1893
Mastacembelus ophidium	Günther	1893
Mastacembelus liberiensis	Steindachner	1894
Mastacembelus loennbergii	Lönnberg	1895
Mastacembelus congicus	Boulenger	1896
Mastacembelus shiranus	Günther	1896
Mastacembelus flavomarginatus	Boulenger	1898
Mastacembelus nigromarginatus	Boulenger	1898
Mastacembelus moorii	Boulenger	1898
Mastacembelus brachyrhinus	Boulenger	1899
Mastacembelus ellipsifer	Boulenger	1899
Mastacembelus paucispinis	Boulenger	1899
Mastacembelus frenatus	Boulenger	1901
Mastacembelus greshoffi	Boulenger	1901
Mastacembelus goro	Boulenger	1902
Mastacembelus sclateri	Boulenger	1903
**Mastacembelus ansorgii*	Boulenger	1905
**Mastacembelus signatus*	Boulenger	1905
Mastacembelus cunningtoni	Boulenger	1906
Mastacembelus longicauda	Boulenger	1907
Mastacembelus batesii	Boulenger	1911
Mastacembelus brevicauda	Boulenger	1911
Mastacembelus reticulatus	Boulenger	1911
**Mastacembelus trispinosus*	Steindachner	1911
Mastacembelus ubangensis	Boulenger	1911
**Mastacembelus moeruensis*	Boulenger	1914
Mastacembelus stappersii	Boulenger	1914
**Mastacembelus laticauda*	Ahl	1937
Mastacembelus albomaculatus	Poll	1953
†*Mastacembelus brichardi*	Poll	1958
Mastacembelus platysoma	Poll & Matthes	1962
**Mastacembelus flavidus*	Matthes	1962
Mastacembelus micropectus	Matthes	1962
Mastacembelus plagiostomus	Matthes	1962
Mastacembelus zebratus	Matthes	1962
**Mastacembelus sanagali*	Thys van den Audenaerde	1972
**Mastacembelus seiteri*	Thys van den Audenaerde	1972
Mastacembelus aviceps	Roberts & Stewart	1976
Mastacembelus crassus	Roberts & Stewart	1976
**Mastacembelus latens*	Roberts & Stewart	1976
Mastacembelus vanderwaali	Skelton	1976
Mastacembelus sp. nov.	Roberts & Travers	(in prep.)

*Unavailable for dissection
†*Caecomastacembelus*
N.B. *Mastacembelus taeniatus* Boulenger, 1901
Mastacembelus victoriae Boulenger, 1903
Mastacembelus mellandi Boulenger, 1914
Mastacembelus mutombotomba Pellegrin 1936
} Synonymised with *M. frenatus* (Matthes, 1962 and Skelton, 1976)

Table 2 Proposed affinities of the Mastacembelidae.

Authority	Date	Relationship
Gronovius	1763	Apodes (Anguilliformes)
Bloch	1786	Apodes (Anguilliformes)
Linneaus	1758	Apodes (Anguilliformes)
Lacépède	1800	Apodes (Anguilliformes)
Schneider (Ed.) *in* Bloch	1801	Apodes (Anguilliformes)
Cuvier & Valenciennes	1831	Notacanthidae
Müller	1844	Scombroidei
Bleeker	1859	*Alostoma* & *Notacanthus*
Günther	1861	'Acanthopterous eels' (in the Blenniformes)
Boulenger	1904	Blenniidae (given separate subordinal status: Opisthomi)
Goodrich	1909	Blenniidae
Regan	1912	Percomorphi (could not trace affinity to any particular group; given separate ordinal status: Opisthomi)
Frost	1930	Percidae
Job	1941	Nandidae
Berg	1940	Acanthopterygii (given separate ordinal status as Mastacembeliformes)
Bertin & Arambourg	1958	Acanthopterygii (given separate ordinal status as Mastacembeliformes)
Bhargava	1953 & 1963*a*	Blennidae
Freihofer	1963	Percoidei
Greenwood *et al*	1966	Perciformes (given separate subordinal rank: Mastacembeloidei)
McAllister	1968	Synbranchidae
Gosline	1971	Synbranchidae

Chaudhuriidae '... so specialised that it plainly deserves the rank of a special order' and assigned it to the Chaudhuriiformes. Sufi (1956) was inclined to agree with Berg (op. cit.), although Greenwood *et al* (1966) retained Chaudhuriidae in the mastacembeloids.

Most recently, Yazdani (1972 & 1975) erected a new genus *Pillaia* for a small eel-like fish collected from the Kasi Hills, Meghalaya. Following more detailed anatomical description and comparison with the Mastacembelidae and Chaudhuriidae, Yazdani (1976*a*) concluded that this genus could be placed in the Mastacembeloidei and erected the Pillaiidae partly as a 'link' between the Mastacembelidae and Chaudhuriidae (Yazdani 1978) and also because of a number of anatomical specialisations including the presence of a single upper jaw element (Yazdani 1976*b*). A second species of Pillaiidae (Talwar, Yazdani & Kundu, 1977) was described from two specimens collected from north east India.

A taxonomic revision of the mastacembelid fishes requires a comprehensive study of their anatomy, particularly that of the African taxa, since existing descriptions, apart from those by Regan (1912: 217–219), Gregory (1933: 353–354), Sufi (1956: 95–96), Poll (1973: 221–230) and Taverne (1973 & 1980), are restricted mainly to accounts dealing with species from the Indian fauna. These include descriptions of cranial development and osteology (Bhargava, 1957*a* & *b*, 1958 & 1963*a*; Maheshwari, 1963 & 1965*a*; Dalela, 1968; Dalela & Garg, 1968; and Yazdani, 1976*a* & *b*), cephalic sensory canals (Maheshwari, 1971), myology (Dubale, 1952), the olfactory system (Bhargava, 1962*a* & *b*), nervous system (Maheshwari, 1965*b*), vascular system (Saxena, 1956; Bhargava, 1963*b*; Agrawal & Dalela, 1966*a*; Maheshwari, 1966*a*; and Dalela, 1967*b*), digestive system (Nagar & Khan, 1957; Agrawal & Tyagi, 1963; Agrawal & Dalela, 1966*b*; and Sriwastwa, 1970), endocrine system

(Khanna & Gill, 1973), excretory system (Chandrasekhar, 1961; and Dalela, 1967*a*), reproductive system (Swarup, Srivastava & Das, 1971; and Maheshwari, 1966*b*) and respiratory system (Datta Munshi, 1964).

This literature contains only scattered and incomplete accounts of the internal anatomy, there are no comprehensive osteological descriptions, and virtually no account of the myology exists.

The Chaudhuriidae and Pillaiidae also lack detailed anatomical coverage, and the numerous errors perpetuated in the literature (e.g. Annandale, 1918; Whitehouse, 1918; Annandale & Hora, 1923; Yazdani, 1976*a* & 1978) and questionable hypothesis regarding their relationships, both taxonomic and phyletic, necessitate a thorough anatomical description of these taxa as well.

This study, therefore, is devoted to detailed osteological descriptions of *Mastacembelus mastacembelus* (and a partial investigation of its cranial myology), *Chaudhuria caudata* and *Pillaia indica*. These descriptions will then form part of a comparative anatomical analysis (including osteology and relevant aspects of cranial myology) of all available mastacembeloid species to provide a basis for a phylogenetic analaysis of the taxa (see Part II; Travers, 1984).

Nomenclatural note

The taxonomic assignment of mastacembeloid species in current use is followed here. However, the succeeding phylogenetic analysis dictates the reclassification of most of these species. Details of these taxonomic changes, including the characters that make them necessary, are given elsewhere (Part II; Travers, 1984).

Material and methods

Material

The spirit collection, stained specimens and dry skeletons of mastacembeloids held at the British Museum (Natural History) together with several specimens presented as gifts, loans from other institutions and a personal collection from Lake Tanganyika, provided the material on which this study is based.

The material examined is listed in full in Table 3, the species arranged alphabetically under their current generic names. All specimens are listed with their registered numbers, together with codes indicating the type of examination or preparation involved, (all are BM(NH) registered specimens unless otherwise indicated). A key to these codes is given in the list of abbreviations on p. 12.

Methods

Osteological studies involved the use of formalin fixed specimens cleared and double stained with Alizarin Red (for bone) and Alcian Blue (for cartilage) following the methods of Dingerkus and Uhler (1977). Myological studies, on the other hand, involved the use of formalin fixed and alcohol preserved specimens. To maximise the usefulness of specimens, where alizarin/alcian transparencies were required, myological examination was performed prior to maceration. Analyses of vertebral structures, fin spines and rays was aided by the use of radiographs. A series of triple-stained transverse histological sections and double-stained longitudinal sections was prepared for more detailed analyses of internal structures.

All specimens were examined with the aid of a Zeiss IVb zoom binocular microscope, fitted with a Schott fibre optic illuminator. Where necessary a substage illumination unit and a camera lucida drawing tube were employed.

The osteological nomenclature is based upon that of Harrington (1955) and Patterson (1977) supplemented by reference to numerous other relevant studies including: Patterson & Rosen (1977) for the ethmoid region, Patterson (1975) for the braincase, Nelson (1969)

Table 3 List of Study Material.

Species	Reg. No.	Preparation
Oriental mastacembeloid taxa		
Genus: *Mastacembelus*		
Mastacembelus alboguttatus	1891.11.30:135–138 (Types)	AP
Mastacembelus armatus	1978.3.2:306–7	A/A
,, ,,	1955.6.22:16–17	MD
,, ,,	LACM 38127–2	MD
,, ,,	1891.11.30:134	DS
Mastacembelus caudiocellatus	1893.6.30:130–132 (Types)	R
Mastacembelus circumcinctus	1980.10.10:274	A/A
,, ,,	1955.6.22:12	MD
,, ,,	1980.10.10:274	R
Mastacembelus erythrotaenia	Unreg	A/A
,, ,,	Unreg	R
Mastacembelus guentheri	1865.7.17:18	MD
,, ,,	1893.3.6:156–157	R
,, ,,	1912.7.20:27	R
Mastacembelus keithi	1938.12.1:267 (Type)	R
Mastacembelus maculatus	1978.3.20:312–314	A/A
,, ,,	1970.9.3:543–552	A/A
,, ,,	1955.6.22:10–11	A
,, ,,	1970.9.3:534–552	A
,, ,,	1970.9.3:543–551	MD
,, ,,	1978.3.20:315	R
Mastacembelus mastacembelus	1974.2.22:1799–1806	A/A, MD & R
,, ,,	1892.9.1:25	DS
,, ,,	1891.6.19:3	R
,, ,,	1955.6.25:4–6 (Types)	R
,, ,,	1975.11.21:8	R
Mastacembelus oatesii	1893.6.30:113–118	A/A
,, ,,	Unreg.	R
Mastacembelus pancalus	1889.2.1:3642–3	A/A
,, ,,	Unreg.	A/A
,, ,,	1935.10.18:71	MD
Mastacembelus sinensis	1927.10.1:19	A/A
,, ,,	1888.3.23:60–2 (Types)	R
,, ,,	1895.5.31:13–14 (Types)	R
,, ,,	IHW-h Gift	R
Mastacembelus unicolor	1978.3.20:317	A/A
,, ,,	1955.6.22:24	R
,, ,,	1978.3.20:318	R
,, ,,	IHW-h Gift	R
Mastacembelus zebrinus	MCZ 9027	A/A
,, ,,	1891.11.30:115–124	A/A & DS
Genus: *Macrognathus*		
Macrognathus aculeatus	Unreg.	A/A
,, ,,	1883.11.28:15	MD
,, ,,	1889.11.12:52	MD
,, ,,	1922.5.19:115	MD & R
Macrognathus aral	1889.2.1:3622–5	A/A
,, ,,	1858.8.15:51–3	R
,, ,,	1872.4.7:38	R
Macrognathus siamensis	Unreg.	A/A
,, ,,	Unreg.	MD
,, ,,	1898.4.2:127–8	R

Table 3 Continued.

Species	Reg. No.	Preparation
Oriental mastacembeloid taxa		
Genus: *Chaudhuria*		
Chaudhuria caudata	MCZ 47058	A/A & AP
,, ,,	1923.3.10:1–3 (Types)	A & AP
,, ,,	ZSI F10822/1	A/A
Genus: *Pillaia*		
Pillaia indica	ZSI (9 ex.)	A/A, A, MD, R & AP
Pillaia khajuriai	ZSI FF816 (Paratype)	AP
African mastacembeloid taxa		
Genus: *Mastacembelus*		
Mastacembelus albomaculatus	Pers. coll.	A/A
,, ,,	MCZ 49212	A/A
,, ,,	Unreg.	R
Mastacembelus ansorgii	1905.5.29:59 (Type)	R
Mastacembelus aviceps	MCZ 50565	A/A
Mastacembelus batesii	1912.6.29:10–16	A/A & MD
,, ,,	1907.5.22:246	DS
Mastacembelus brachyrhinus	MCZ 50563	A/A
Mastacembelus brevicauda	1904.7.1:250	A/A
,, ,,	1906.5.28:193–196 (Types)	R
Mastacembelus brichardi	1976.5.21:99–108	A/A & MD
,, ,,	MCZ 50255	A/A
Mastacembelus congicus	1975.6.20:696–697	A/A
,, ,,	1901.12.26:64	MD
,, ,,	1899.6.28:23	DS
Mastacembelus crassus	MCZ 50258	A/A
Mastacembelus cryptacanthus	1866.6.26:11 (Type)	R
Mastacembelus cunningtoni	Unreg.	A & R
Mastacembelus ellipsifer	Pers. coll.	A/A & MD
Mastacembelus flavidus	RG 130435–439	R
,, ,,	1906.9.8:273 (Type)	R
Mastacembelus flavomarginatus	1912.4.1:575–579	A/A & MD
Mastacembelus frenatus	1961.12.1:356–7	A/A
,, ,,	1977.6.9:134–6	A/A
,, ,, (*mellandi*)	RG 79-01-P-6335–339	A/A
,, ,, (*taeniatus*)	RG 91437	A/A
Mastacembelus goro	1937.4.16:18–22	A/A
Mastacembelus greshoffi	1958.9.8:287	A/A
,, ,,	Unreg.	R
Mastacembelus liberiensis	RG 73.10.P-7363-372	A/A
Mastacembelus loennbergii	1969.3.26:68–69	A/A
,, ,,	1904.1.20:71	R
,, ,,	Unreg.	HS
Mastacembelus longicauda	1910.2.23:7–10	A/A & MD
,, ,,	1908.5.20:189 (Type)	R
Mastacembelus marchii	MCZ 50590	A/A
Mastacembelus marmoratus	RG 118712–719	A/A
Mastacembelus micropectus	MCZ 49210	A/A
,, ,,	RG 130804–812	A/A
Mastacembelus moorii	1955.12.20:1685	A/A
,, ,,	MCZ 50838	A/A

Table 3 Continued.

Species	Reg. No.	Preparation
African mastacembeloid taxa		
Mastacembelus niger	137360–365	A/A
Mastacembelus nigromarginatus	1969.4.28:11–12	A/A
Mastacembelus ophidium	1968.123.30:4	A/A
,, ,,	1936.6.15:1753–6	A/A
Mastacembelus paucispinis	1976.5.21:119–129	A/A
,, ,,	RG 178099	A
Mastacembelus plagiostomus	Pers. coll	A/A
Mastacembelus platysoma	RG 78–25–P.34–38	A/A
Mastacembelus reticulatus	1932.5.18:105–6	A/A
,, ,,	Unreg.	R
Mastacembelus sclateri	904.7.1:104–105	A/A
,, ,,	1911.5.30:35	DS
,, ,,	1909.4.29:111	R
,, ,,	1911.5.30:38	R
Mastacembelus shiranus	Unreg.	A/A
,, ,,	1969.2.20:3–12	A/A
Mastacembelus signatus	1905.11.10:13 (Type)	R
Mastacembelus stappersii	RG 152167	A
Mastacembelus tanganicae	Pers. coll.	A/A
,, ,,	1968.12.30:2–3	A/A
,, ,,	MCZ 49209	A/A
Mastacembelus ubangensis	RG 124267–268	A/A
Mastacembelus vanderwaali	1977.2.3:168–172	A/A
,, ,,	AM 3450	A
Mastacembelus zebratus	MCZ 49211	A/A
,, ,,	RG 130800–801	R
Mastacembelus sp. nov.	CAS Gift	A/A

for the branchial arches, and Greenwood & Rosen (1971) and Rosen (1973) for the caudal skeleton. The nomenclature of muscles follows that of Winterbottom (1974), and cranial nerves that of Freihofer (1978).

Abbreviations

Abbreviations used in text figures and tables.

Skeletal elements

Aa	Anguloarticular
AAPP	*Adductor arcus palatini* process
ACh	Anterior ceratohyal
ADPt	Anal fin distal pterygiophore
AFR	Anal fin ray
AHS	Autogenous haemal spine
AP	Anterior process
AP+MPt	Anal proximal and medial pterygiophores
AS	Anal spine
ASPt	Anal spine supporting pterygiophore
Bb 1–4	Basibranchial 1 to 4
Bblk	Basibranchial 1 keel
BblkC	Basibranchial 1 keel with cartilaginous ventral edge
Bb2VP	Basibranchial 2 ventral process
Bb2VPA	Basibranchial 2 ventral process arched

Bh	Basihyal
BLF	Baudelot's ligament fossa
Bo	Basioccipital
Bpt	Basipterygia
BR	Branchiostegal ray
Bs	Basisphenoid
C	Cleithrum
Cb 1–5	Ceratobranchial 1 to 5
Cb5MP	Ceratobranchial 5 muscular process
Cb5Tp	Ceratobranchial 5 toothplate
Ck	Cleithrum keel
Cmen	Cartilage meniscus
CMF	Cancellous medial face of lateral ethmoid
CN	Cartilage nubbin
Com	Coronomeckelian
Cor	Coracoid
CVt 1	1st Caudal vertebra
D	Dentary
DCP	Dentary coronoid process
DDPt	Dorsal fin distal pterygiophore
DFR	Dorsal fin ray
DHh	Dorsal hypohyal
DP	Dorsal process
DP+MPt	Dorsal proximal and medial pterygiophore
DPP	Dentary posterior process
DPt	Distal pterygiophore
DS	Dorsal spine
DSP	Dentary symphysial process
DSPt	Dorsal spine supporting pterygiophore
E 1–3	Epural 1 to 3
Eb 1–4	Epibranchial 1 to 4
EC	Ethmoid cartilage
EcR	Epicentral rib
Ect	Ectopterygoid
End	Endopterygoid
EndAP	Endopterygoid anterior process
ENS	Expanded (anteroposteriorly) neural spine
Ep	Epioccipital
EpR	Epipleural rib
Ex	Exoccipital
ExDP	Exoccipital dorsal perforations
Exsc	Extrascapula
ExVE	Exoccipital ventral extension
F	Frontal
FDL	Frontal descending lamina
FF	Facial foramen
Fn	Fenestra
FP	Frontal pedicel
FPb2	Fragmented pharyngobranchial 2
FPmAS	Fragmented premaxilla alveolar surface
FTp	Fused toothplate
GTS	Gutter in lateral ethmoid for *truncus supraorbitalis*
H 1–6	Hypural 1 to 6
HAF	Hyoid artery foramen
Hb 1–3	Hypobranchial 1 to 3
Hb3AP	Hypobranchial 3 anterior (descending) process
Hb3Tp	Hypobranchial 3 toothplate
HHAVt (1)	Hemispherical head of 1st abdominal vertebra
HP	Hypural plate

HS	Haemal spine
Hyo	Hyomandibula
HyoAF	Hyomandibular anterior flange
HyoS	Hyomandibular spur
ICF	Internal carotid foramen
Ih	Interhyal
InP	Interdigitating process
Io 1–6	Infraorbital 1–6
IoAP	Infraorbital 1 anterior process
IoPP	Infraorbital 1 posterior process
LC	Lateral commissure
LCF	Lateral commissure flange
LE	Lateral ethmoid
LEVF	Lateral ethmoid ventral facet
LEVP	Lateral ethmoid ventral process
LP	Lateral parapophysis
MC	Meckel's cartilage
Met	Metapterygoid
Mx	Maxilla
N	Nasal
NA	Neural arch
NAF	Neural arch foramen
NS	Neural spine
Op	Operculum
OPM	Opening for the posterior myodome
P	Parasphenoid
Pal	Palatine
PaLS	Palatine spur
PalSF	Palatine suborbital flange
PalT	Palatine teeth
Par	Parietal
Pb 2–4	Pharyngobranchial 2 to 4
PCh	Posterior ceratohyal
PCR	Principal caudal fin rays
PFR	Pectoral fin rays
Ph	Parhypural
Pm	Premaxilla
PmAP	Premaxilla ascending process
Pop	Preoperculum
Poz	Postzygapophysis
PP	Postorbital process
PPP	Parasphenoid posterior process
Pr	Prootic
PR	Pleural rib
PrAP	Prootic anterior process
Prorb S	Preorbital spine
PrS	Prootic spur
PrSh	Prootic shelf
Prz	Prezygapophysis
Pt	Pterosphenoid
PtN	Pterosphenoid notch
PtP	Pterosphenoid pedicel
PtT	Posttemporal tubule
Pu 2 & 3	Preural centra 2 to 3
Pu+U	Fused ural and 1st preural centra
Q	Quadrate
R 1–4	Radials (actinosts) 1–4
Ra	Retroarticular
ROSFF	*Ramus opercularis superficialis facialis* foramen

SB	Saccular bulla
Sc	Scapula
ScaF	Scapular foramen
Snl	Supraneural lamina
So	Supraoccipital
SoC	Supraoccipital commissure
Sop	Suboperculum
SorC	Supraorbital sensory canal commissure
Sph	Sphenotic
SphAF	Sphenotic anterior flange
StSC	Supratemporal sensory canal
Sue	Supraethmoid
Sym	Symplectic
TF	Trigeminal foramen
TFF	Trigeminal and facial foramen confluent
TP4	Toothplate 4
TPOlfT	Tubular passage for olfactory tract
U 1–2	Uroneural 1 to 2
Uh	Urohyal
UhAP	Urohyal ascending process
UhF	Urohyal facet
Unc	Uncinate process
UTp	Unfused toothplate
V	Vomer
VCPH	Vascular canal in head of parhypural
VHh	Ventral hypohyal

Muscles and soft tissues

A_1, A_2, A_3 & A_w	Parts of the *adductor mandibulae*
$A_{2\alpha}$ & $A_{2\beta}$	Deep and superficial subdivisions, respectively, of part A_2 of the *adductor mandibulae*
AAP	*Adductor arcus palatini*
A_wApo	Tendinous aponeurosis of part A_w of the *adductor mandibulae*
A Hyo	*Adductor hyomandibulae*
AO	*Adductor operculi*
B Lig	Baudelot's ligament
DO	*Dilatator operculi*
Epax	*Epaxialis* musculature
Hyo Abd	*Hyohyoidei abductores*
Hyo Add	*Hyohyoidei adductores*
Int	*'Musculus intraoperculi'*
LAP	*Levator arcus palatini*
LO	*Levator operculi*
MmLig	Maxillo-mandibular ligament
ObSup	*Obliquus superioris*
Olft	*Nervus olfactorius*
Pseu	Pseudobranch
RMT	*Ramus mandibularis trigeminus*
tA_1, $tA_{2\alpha}$, $tA_{2\beta}$, tA_3 & tA_w	Tendons from parts of the *adductor mandibulae*
TI	*Truncus infraorbitalis*

Note on the figures: even stipple-dots indicate the presence of cartilage. The scale on all figures indicates 1 mm.

Table of study material

A/A	Double alizarin red/alcian blue stained transparency
A	Alizarin stained transparency
HS	Histologically stained and sectioned
MD	Muscle dissection (cheek and opercular region)

DS	Dry skeleton preparation
R	Radiograph
AP	Alcohol preserved specimen not available for dissection or preparation (superficial gross morphology examined only)
Unreg.	Unregistered specimen held at BM (NH)
Pers. coll.	Personally collected specimen held at BM(NH)

Institutional abbreviations

AM	Albany Museum, Grahamstown
BM(NH)	British Museum (Natural History)
CAS	California Academy of Sciences
IHW-h	Institute of Hydrobiology, Wuhan (China)
LACM	Natural History Museum of Los Angeles County
MCZ	Museum of Comparative Zoology, Harvard
RG	Koninklijk Museum voor Midden-Afrika, Tervuren
ZSI	Zoological Survey of India

Osteology of *Mastacembelus mastacembelus*

Although *Mastacembelus mastacembelus* (Banks & Solander, *in* Russell, 1794) is the type species of the genus (Wheeler 1956) it has not been subjected to a detailed anatomical study. This description is based on two double stained specimens (standard length 212 mm. and 217 mm.) and a single skeletal preparation (see Table 3).

Neurocranium

Ethmovomerine region

Of the two median endochondral ethmoid bones identified by Patterson & Rosen (1977) only the *supraethmoid* is present in *M. mastacembelus.* The supraethmoid is a laterally compressed bone that caps the anterodorsal part of the ethmoid region (Fig. 1a). It consists of two regions; anteriorly, a thin median septum separates the olfactory sacs and posteriorly a long posterodorsally directed process lies between the anteromedial face of each frontal. The anteroventral edge of the median septum is fused to the vomer, and the anterodorsal edge is enlarged to form an ovoid prominance for the attachment of ligaments which help govern the movement of the rostral appendage. Below the posterodorsal process the lower corner of the supraethmoid is cartilaginous and extends as a septal cartilage along the anterodorsal surface of the parasphenoid (below the lateral ethmoids) into the orbital cavity (Fig. 1a).

The *vomer* is a long bone and consists of a broad faceted head region and a long posterior shaft (Fig. 1a & b). Both the anterior and anterolateral faces of the vomerine head are faceted; they articulate with the rostral appendage and medial face of the short ascending process from the premaxilla, respectively. The vomerine shaft lies in a groove on the underside of the parasphenoid and extends posteriorly to a point adjacent to the anterior edge of the pterosphenoid. The dorsal surface, posterior to the median supraethmoid septum, contacts the ventral surface of the posterior cartilaginous region of the supraethmoid. Vomerine teeth are absent.

Each *Lateral ethmoid* is connected to its partner in the midline, and together they saddle the cartilaginous region of the supraethmoid. There is no anterior myodome between the lateral ethmoids. The medial wall is compressed into a cancellous bony sheet that contacts its partner in the midline anterodorsal to the cartilaginous end of the supraethmoid. This wall, together with the outwardly convex lateral wall gives the lateral ethmoid a tubular central region (Fig. 2). The olfactory sac is hypertrophied and its posterior end lies within the anterior entrance to this tubular centre of the lateral ethmoid. The posterior opening accommodates the broad *nervus olfactorius* (Freihofer, 1978), which runs directly from the olfactory bulb to the nasal organ.

The dorsal edge of the lateral ethmoid consists of an anterior arm which lies below the posteroventral surface of the nasal, and a posterior arm that lies below the anteroventral surface of the frontal. A gutter runs longitudinally along the dorsomedial face and carries part of the *truncus supraorbitalis* nerve prior to its separation into two main rami. A large rounded condyle on the lateral face of the lateral ethmoid articulates syndesmotically with the posterior ascending process on the 1st infraorbital bone. Ventral to this condyle is a facet which articulates synchrondrally with the anterior end of the suspensorium (the anterodorsal edge of the ectopterygoid and anterior tip of the endopterygoid).

The *nasal* is a large, thin, flattened bone inclined to the vertical, and overlies the long olfactory cavity (Fig. 1a & c). The medial edge is joined by connective tissue to the dorsolateral margin of the supraethmoid. Posteriorly, it overlaps the anterodorsal process of the lateral ethmoid and contributes, with the 1st infraorbital, to the rim of the posterior nostril.

The dorsolateral margin of the 1st infraorbital is overlapped by the lateral edge of the nasal, and the two are joined by connective tissue.

The nasal encloses the anterior region of the supraorbital sensory canal which forks anteriorly, the short lower arm terminating in a pore on its anterolateral surface.

Orbital region

The *pterosphenoid* is a major contributor to the long, precommissural lateral wall of the braincase. Its anterior edge contributes to the posterior rim of the orbital cavity and partly surrounds the optic foramen (Fig. 1a & b). The anterodorsal edge of the lateral wall is grooved, and accommodates the ventral edge of the frontal descending lamina. Posteriorly, the dorsal margin of the pterosphenoid is partly overlapped by the posterior margin of the frontal lamina and the anterolateral flange of the sphenotic.

The ventral edge of the pterosphenoid is curved medially and sutured to its partner in the midline. Together, these bones form the ventral rim of the optic foramen and roof the small posterior myodome, giving this region of the neurocranium a somewhat tubular shape.

The posterior edge of the pterosphenoid lies between the sphenotic and prootic, and contributes to the rim of the trigeminal foramen. The lateral face of the pterosphenoid is overlain by a long anterior process on the prootic. Dorsal to this process the pterosphenoid is grooved longitudinally to accommodate the nerves issuing from the trigeminal foramen.

The *basisphenoid*, the smallest bone in the neurocranial complex is depressed and Y-shaped. Its small size is the result of its compression between the ventral face of the median pterosphenoid symphsis and the dorsal surface of the parasphenoid (Fig. 1a). The tip of each dorsal arm of the basisphenoid contacts a pterosphenoid. A short ventral shaft extends downwards towards the parasphenoid as a thin process dividing the posterior myodome.

The *parasphenoid* is the longest bone in the neurocranium and extends from below the lateral ethmoids to the posterior edge of the basicranium (Fig. 1a & b). It consists of two main regions: a long anterior process bridging the orbital cavity (between the otic and nasal areas) and a longitudinal, trough-like, posterior region. The ventral surface of the anterior region is grooved to accomodate the vomerine shaft. A dorsal median ridge on the anterior part of the parasphenoid meets the membranous interorbital septum. The lateral wall of the posterior trough-like region overlaps the ventrolateral margin of the prootic; it is not developed into an ascending process. A notch in the dorsal edge of the parasphenoid (ventral to the lateral commissure in the prootic) forms, with the ventral edge of the prootic, the internal carotid foramen. The posteroventral face of the parasphenoid divides into a pair of processes which lie longitudinally on either side of a basioccipital ridge and extend to the posterior margin of that bone.

The *infraorbital* series consist of one large element–the 1st infraorbital (lachrymal)–and 5 small tubules (2nd to 6th infraorbitals). The infraorbital sensory canal is enclosed within these elements (Fig. 3).

The 1st infraorbital is expanded posteriorly and tapered anteriorly, extending to the tip of the nasal. Two large pores are present, as well as several irregular branches of the infraorbital sensory canal system which terminate in small pores on the lateral face of the bone.

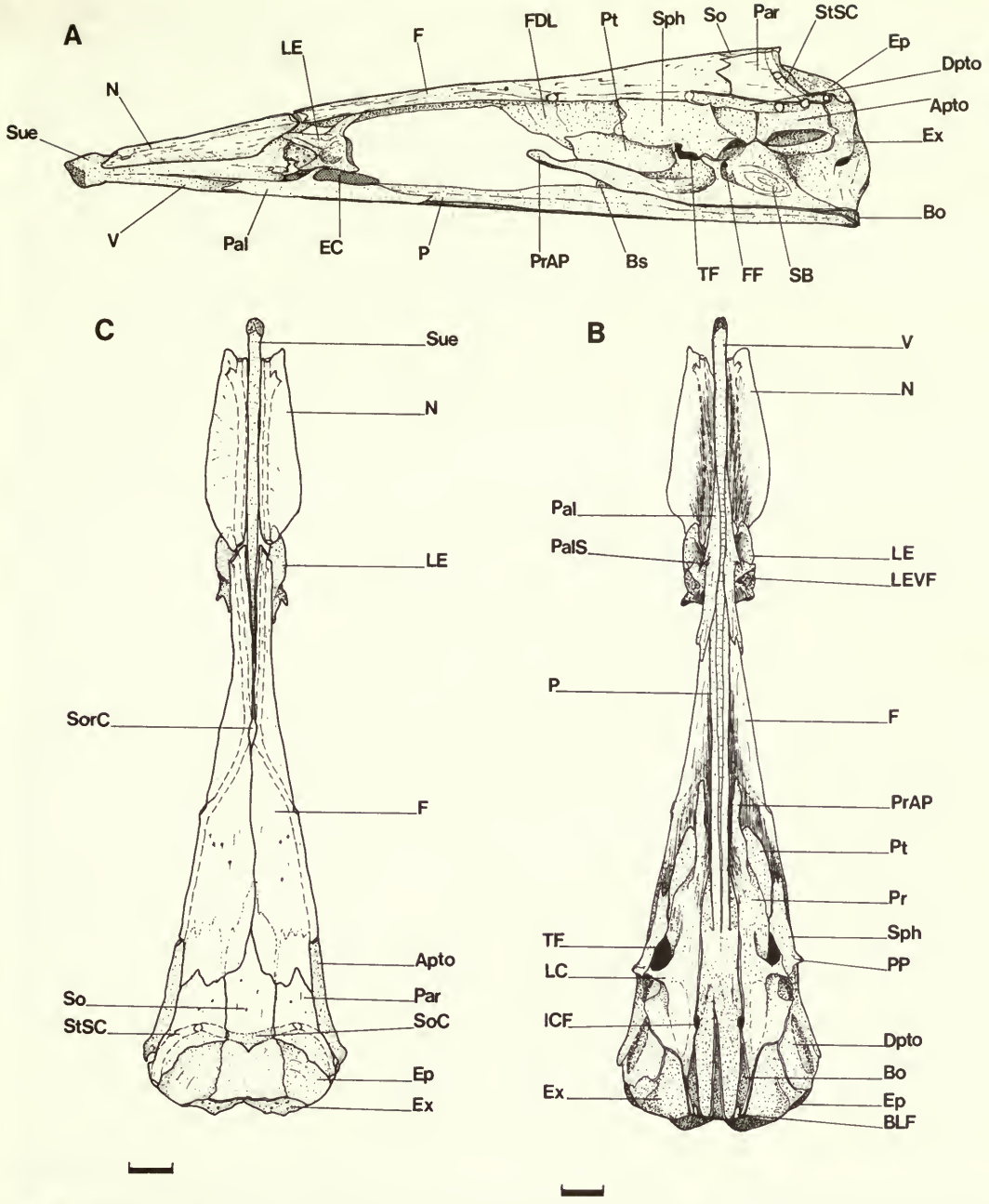


Fig. 1 *Mastacembelus mastacembelus*, neurocranium in: (a) lateral view of left side; (b) ventral view and (c) dorsal view.

The posterodorsal edge of this bone is developed into two ascending processes. The dorsomedial face of the larger posterior process is faceted and joined syndesmotically with the rounded condyle on the lateral ethmoid. A small lip on the anterior edge of the ascending process also contacts the lateral ethmoid. The smaller ascending process is joined by epidermal tissue to the posteroventral edge of the nasal; together with the larger process it forms the ventral rim of the posterior nasal opening.

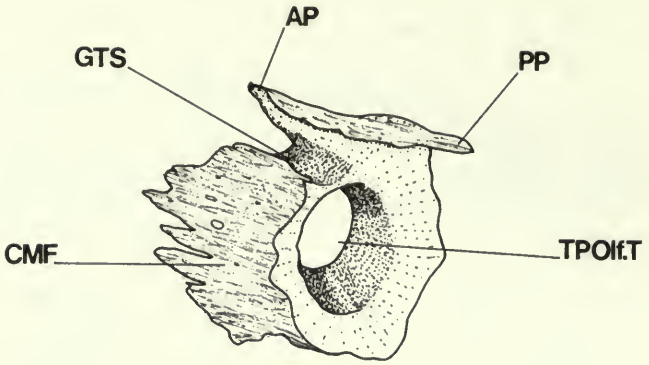


Fig. 2 *Mastacembelus mastacembelus,* right lateral ethmoid in posteromedial view.

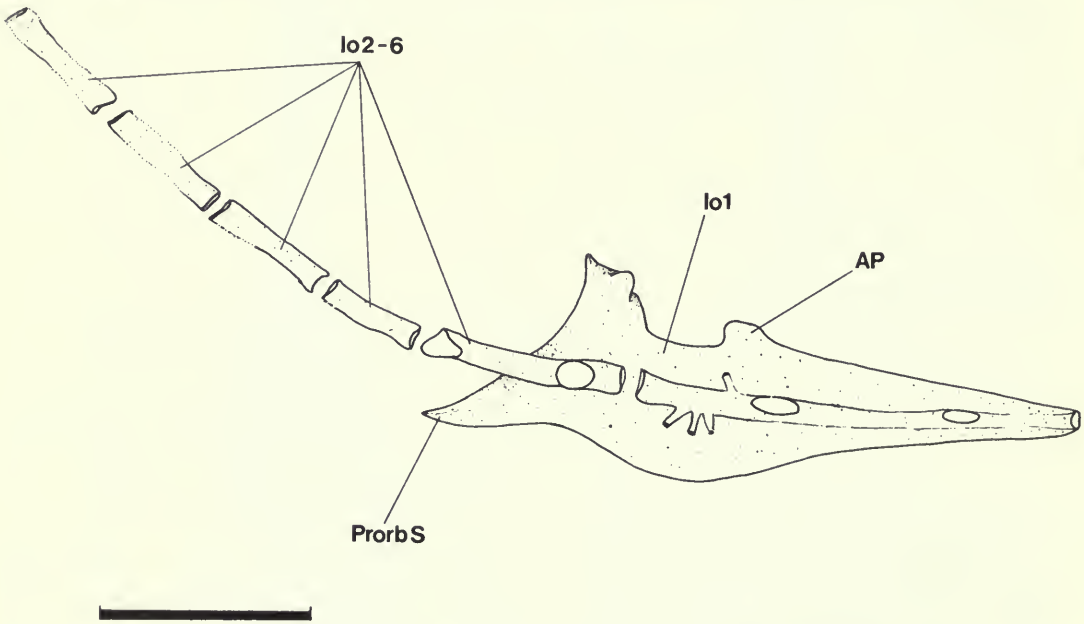


Fig. 3 Infraorbital series of *Mastacembelus mastacembelus.*

The ventral edge of the bone tapers posteriorly to a distinct, pointed process (preorbital spine; Fig. 3), which pierces the integument ventral to the 2nd infraorbital tubule.

The remaining infraorbital bones are reduced to ossifications around the sensory canal. The 2nd element partly overlaps the posterolateral face of the 1st, and has a single large pore midway along its length. The sensory canal portions of the 4th, 5th and 6th infraorbitals are decreasingly ossified.

Otic region

The *prootic* is the largest endochondral bone enclosing the cranial cavity, and in addition to its main posterior region has a prominent anterior process extending into the orbit (Fig. 1a & b).

This region of the prootic overlaps the dorsolateral margin of the parasphenoid and in so doing obscures the basisphenoid laterally. A fossa in the dorsolateral margin of the prootic combines with a similar one in the ventrolateral margin of the sphenotic to form the socket for the anterior hyomandibular condyle. Posterior to the socket, the prootic is bevelled posteroventrally and is connnected dorsally to the pterotic by a number of dentate sutures; ventrally it is connected to the anterolateral edge of the exoccipital and the anterodorsal edge of the basioccipital.

The posterolateral face of the bone is bullate and accommodates the small sacculus in its entirety. The trigeminofacialis chamber is situated anterior to the saccular bulla. The large trigeminal foramen lies anterior to the slender lateral commissure (Fig. 1a), whilst the facial foramen, which is small (relative to the size of the trigeminal foramen), generally pierces the prootic medial to the lateral commissure.

The trigeminal foramen is bounded by the sphenotic (dorsally) and the prootic (ventrally). A short descending spur from the ventral edge of the sphenotic lies above the tip of a similar spur rising from the dorsal edge of the prootic. These spurs do not contact one another; together with the posterior edge of the pterosphenoid they form the rim of the trigeminal foramen. Medial to the trigeminofacialis chamber the prootic bears a vertical strut pierced by the inner opening of the facial foramen. Dorsally, this medial strut contacts the sphenotic, and ventrally it meets its partner in the midline. A hollow, gutter-like channel longitudinally indents the ventromedial face of the strut. The internal carotid artery runs along this channel from the small, posterior myodome and leaves through a foramen situated along the prootic/parasphenoid junction, ventral to the lateral commissure. A narrow, longitudinal ridge on the anterolateral face of the prootic is continuous with the lower edge of a groove in the ventrolateral face of the pterosphenoid, and supports the *truncus infraorbitalis*.

The large *sphenotic* is a major element in the dorsolateral wall of the braincase (Fig. 1a & b). It is characterised by a prominent, anterolateral flange which overlies its medial, sutured, connection to the pterosphenoid. Anterolaterally, the sphenotic contacts the frontal descending lamina by which it is excluded from contributing to the orbital border. Dorsally the sphenotic is grooved and accommodates the ventrolateral edge of the frontal. The posterolateral edge of this groove forms the postorbital process (dorsal to the lateral commissure), from which the *dilatator operculi* muscle originates. The posterior position of this postorbital process (relative to the orbit) illustrates the extreme attenuation of the precommissural region of the neurocranium. The posterior and posterodorsal edge of the sphenotic is overlapped by the prootic. A wide dorsomedial flange extends below the pterotic, to contact the ventral surface of the parietal. Below its postorbital process the sphenotic is sutured to the dorsal surface of the lateral commissure and anterior to this forms the upper border of the trigeminal foramen. The medial face of the sphenotic accommodates the anterior semicircular canal which is looped through the bone, forming the *pons moultoni*.

The *pterotic* consists of two portions; the ventral autopterotic and the dorsal dermopterotic (Fig. 1a & c). The autopterotic is connected to the sphenotic anteriorly, the prootic ventrally, with the exoccipital and epioccipital posteriorly. The dorsal edge of this region is fused to the ventral edge of the dermal portion of the pterotic.

The main body of the pterotic encloses the horizontal semicircular canal, and as a result its lateral face is bullate; its ventral surface is grooved to accommodate the posterior hyomandibular head.

There is no posttemporal fossa although the ventral margin of the pterotic forms part of a recess in the lateral wall of the basicranium.

The dermopterotic extends anteriorly between the sphenotic and frontal. Its anterior tip and posterodorsal edge are sutured to the lateral edge of the parietal. The temporal junction between the supraorbital, preopercular and posttemporal sensory canals is contained in the dermopterotic.

The *epioccipital* is small and forms, with the exoccipital and supraoccipital, the posterodorsal wall of the basicranium (Fig. 1a & c).

Dorsally, it is overlapped by the posterior edge of the parietal. An artery which supplies

the *epaxialis* musculature leaves the cranial cavity *via* a small foramen midway along the parietal/epioccipital border. Ventrally, the epioccipital is bounded largely by the exoccipital, to which it is sutured, and partly by the pterotic.

The inner aspect of the epioccipital contains the posterior semicircular canal and this imparts a bullate appearance to the bone's posteroventral face. The dorsal surface of this bulla forms the floor of a shallow fossa on the posterior face of the epioccipital (lateral to the posterodorsal foramen). A large, partly ossified tendon from the epaxial musculature inserts in this fossa.

Each *exoccipital* is an irregularly shaped bone and is a major contributor to the posterior wall of the neurocranium (Fig. 1a). Above the foramen magnum a dorsomedially directed process is connected in the midline to its partner by a pair of dentate processes. This symphysis, combined with a ventromedial one, results in the exoccipitals completely surrounding the foramen magnum.

The complex anterior edge of the exoccipital connects, by thin interdigitating sheets of bone, with the epioccipital dorsally, the pterotic laterally, and the prootic ventrally. The junction between these elements lies within the recess in the lateral wall of the basicranium (from which originate the branchial levator muscles).

The ventral surface of each exoccipital is flat and abuts against the dorsolateral surface of the basioccipital. Posteroventrally, they have prominent, concave, deltoid facets. These facets, in combination with a similar shaped facet on the posterior face of the basioccipital, form the occipital facet (a concave socket) which articulates with the 1st abdominal vertebra.

The inflated appearance of the anterolateral wall is a result of an inner recess in the exoccipital.

Three major foramina perforate the exoccipital. The small glossopharyngeal foramen pierces the bullate anterolateral wall, a large subdivided foramen, for branches of the occipito-spinal nerve, lies posterior to that for the glossopharyngeal nerve, whilst between, and slightly dorsal to them, lies the vagal foramen.

The stout *basioccipital* is approximately rectangular in outline (Fig. 1b). Its dorsal surface is pyramidal, with the four raised faces converging dorsally to form a longitudinal ridge. The anterodorsal face is excavated to form a pair of pit-like fossae, the *cavum utriculae.* The faceted and concave posterodorsal face contributes to the tripartite occipital facet (see above). The ventral surface of the basioccipital is flat except for a low, central, longitudinal ridge which separates the posterior processes of the parasphenoid.

The *posterior myodome* is small in comparison with that in other perciforms. It is roofed by the medial process of the pterosphenoids and divided in the midline by the ventral shaft of the basisphenoid.

The *supraoccipital* is a flattened bone and may be divided topographically into two regions: (1) the anterior horizontal part and (2) the sloped posterior region which is inclined at 45° to the former (Fig. 1c).

A supraoccipital crest is absent. The dorsal surface is transversely convex and bounded on either side by the parietals and by a posterior portion of the frontals. All these surrounding bones cover the supraoccipital margin. Crossing its posterior surface is a gutter-like channel which accommodates the supratemporal sensory canal commissure. The posterior portion of the supraoccipital is bordered laterally by the epi- and exoccipitals. Ventrally, its tip meets the exoccipital dorsal symphysis by which it is excluded from the foramen magnum.

The *frontal* is the major roofing bone of the cranium and is comprised of two regions: dorsally a flat, horizontal roofing region and ventrally a descending vertical lamina (Fig. 1a & c).

The dorsal region of the frontal is particularly attenuated and narrows above the orbit. Its flat surface lacks crests or any form of sculpturing. Anteriorly, it overlies the posterior tip of the ventral ethmoid, and posteriorly it overlaps the anterior margin of the supraoccipital. Beneath the anterior end of the frontal, and joined to it by connective tissue, is the posterodorsal arm of the lateral ethmoid (see above). The posterior end of the dorsal region of the frontal, overlaps a wide bony lip on the anterior edge of the parietal and con-

nects posterolaterally with the dorsal edge of the pterotic and the sphenotic. The lateral edge of the frontal curves ventrally and is concave above the orbit. Medially, the frontals meet along a straight suture.

The frontal sensory canal (supraorbital branch of cephalic system) passes along the lateral margin of the bone. Posterior to the orbit the ascending infraorbital canal connects with the supraorbital canal, its junction indicated by a large pore in the lateral edge of the frontal.

Anterior to this point the supraorbital canal opens through a medial pore which marks an anterior commissure between the canals from either side of the neurocranium (Fig. 1c).

The frontal descending lamina contributes to the postorbital lateral wall of the braincase (Fig. 1a). Its anterior edge forms, with the pterosphenoid, the posterior rim of the orbit. The ventral lamina, together with the dorsal region of the frontal and the pterosphenoids enclose the optic foramen. The ventral edge of the lamina overlaps the lateral face of the pterosphenoid, and posteriorly is sutured to the anterolateral edge of the sphenotic.

The *parietal* is approximately square in outline except for a short posterolateral arm (Fig. 1a & c). Anteriorly, a wide bony lip is overlapped by the frontal; posteriorly it is sutured to the dorsal edge of the epioccipital. Laterally, the parietal is joined to the pterotic and posterodorsal flange of the sphenotic, whilst medially it contacts the supraoccipital.

The unsculptured dorsal surface of the parietal is flat except for a slight curvature of its ventrolateral aspect. A sensory canal (supratemporal branch) crosses within the posterodorsal margin, from its lateral (pterotic/posttemporal) to its medial (commissure) connections. A single, large pore on this canal pierces the posterodorsal surface of the parietal.

Extrascapular bones are absent.

Two small ossified dermal tubules lie equally spaced along the postcranial sensory canal between the tip of the posterolateral arm of the parietal and the dorsal tip of the supracleithrum. These tubules represent the only ossified remnants of the *posttemporal* bone (Fig. 11).

Jaws

Upper Jaw

The *premaxilla* is a weakly curved, rod-like element, characterised by its short ascending process (Fig. 4). The bone's dorsal edge is tightly joined to the ventral face of the maxilla

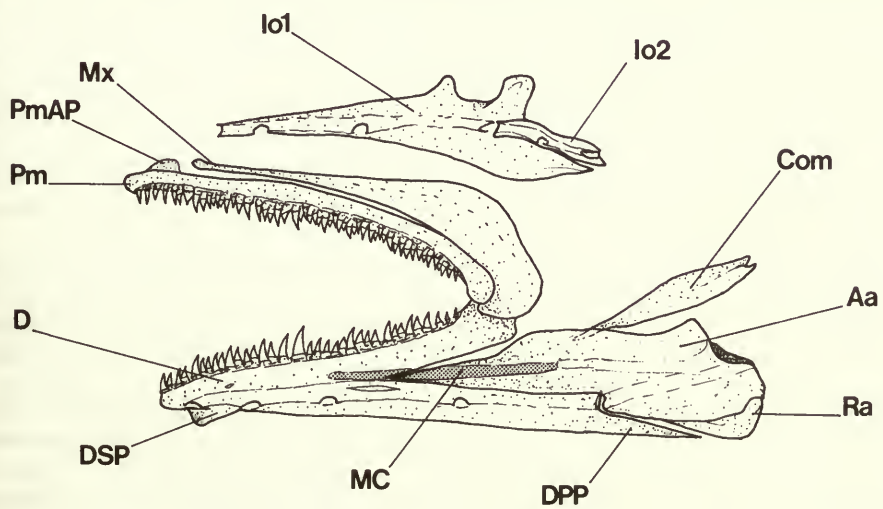


Fig. 4 *Mastacembelus mastacembelus,* lateral view of left upper and lower jaw bones with 1st and 2nd infraorbitals.

by a broad sheet of connective tissue. Anteriorly, each premaxilla curves medially (below and beyond the anterior end of the maxilla) to form a midline symphysis. The short stump-like ascending process articulates (*via* a facet on its medial face) with the faceted anterolateral end of the vomer. The premaxillae are not protrusible.

Its posteroventral end is laterally compressed and partly overlaps the ventral flange of the maxilla. The tooth-bearing alveolar surface of the premaxilla is broadest anteriorly and tapers posteriorly. The dentition is in the form of large, acrodont, caniniform teeth with posteriorly directed tips. Tooth attachment (to the premaxilla, dentary and pharyngeal bones) is by a ring of collagen between the tooth base and bone, in a mode equivalent to type 2 described by Fink (1981). The teeth are arranged in 1–8 irregular rows (depending upon the position along the premaxilla) and decrease in size medially.

The *maxilla* tapers anteriorly to a blunt tip which is connected, *via* a short ligament, to the posterior edge of the premaxillary ascending process and medially to the lateral facet on the head of the vomer. Posteriorly, the maxilla is thickened and expanded ventrolaterally to form an extension which, when the jaws are adducted, overlies the lateral face of the coronoid process (Fig. 4). This wide posterior region of the maxilla is joined to the coronoid process by a medial sheet of connective tissue. The dorsal edge is loosely joined by epidermal tissue to the ventromedial margin of the 1st infraorbital, and the ventral edge is connected firmly to the dorsal edge of the premaxilla.

Lower Jaw

The *dentary* is a long bone and although straight is directed mesad. Its symphysis lies posterior to the median connection of the premaxilla and there is a low symphysial projection on its anteroventral edge.

The dentary divides, posterolaterally, into an upper coronoid and a lower ventral arm. The coronoid region is developed posteriorly into a relatively tall, shallow coronoid process (Fig. 4). The long and narrow dorsal surface anterior to the coronoid process is alveolate and toothbearing. This toothed surface contains 3 rows of caniniform acrodont teeth, those of the outer row being somewhat larger than the inner teeth. The alveolar surface narrows posteriorly and does not extend onto the coronoid process.

The dentary portion of the mandibular sensory canal opens to the surface of the bone through four pores. The posteroventral region of the dentary extends below and beyond the point at which the sensory canal enters the dentary. The dorsal surface of this posteroventral projection (Fig. 4) is grooved and accommodates the ventral edge of the anguloarticular and the anteroventral edge of the retroarticular. The ventral edge of the lower jaw is, therefore, almost entirely formed by the dentary.

The long *anguloarticular* (Fig. 4) is characterised by two unusual features: the presence of a straight dorsal edge with no ascending process, and by the size and dorsal position of the coronomeckelian.

The anterior end of the anguloarticular lies between the coronoid and the ventral limb of the dentary. The posterodorsal edge is capped by a wide, transverse facet that receives the anterior condyle of the quadrate in a euarthroidal joint. On the posteromedial face of the anguloarticular is a small rounded ridge (ectosteal plate). Meckel's cartilage lies between the anterior end of this ridge and the dentary.

The *retroarticular* is a small L-shaped bone connected to the posteromedial face of the anguloarticular. It lies below the dorsal facet on the anguloarticular to which it is connected synchondrally.

The *coronomeckelian* (sesamoid articular) is particularly large and uniquely positioned (Fig. 4) in comparison with its size and position in other teleostean fishes.

It is long, narrow and tapers at both anterior and posterior ends. The anterior end overlaps the dorsomedial margin of the anguloarticular and is connected to its medial face, dorsal to Meckel's cartilage. From this point the coronomeckelian extends posterodorsally across the anterolateral face of the suspensorium. The posterior end lies lateral to the junction of

the ectopterygoid with the quadrate. The anteroventral tendon of part A_3 of the *adductor mandibulae* muscle inserts on to the posterior end of the coronomeckelian and the *ramus mandibularis trigeminus* (part of the Vth cranial nerve) passes downwards, along its ventral edge (Fig. 4), to extend anteriorly into the dentary.

Hyopalatine arch

The stout *hyomandibula* has its dorsal surface produced into two articular heads separated by a shallow depression (Fig. 5). The anterior condyle has a synchondral articulation (*via* a cartilaginous meniscus) with the anterior, prootic-sphenotic fossa on the lateral wall of the neurocranium. The larger, posterior condyle is ellipsoidal and fits into the channel-like pterotic fossa with which it articulates synchondrally.

The ventral part of the hyomandibula is a broad shaft; its tip is cartilage-capped and joined syndesmotically with the posterior end of the symplectic. The anterior edge of this shaft bears a small descending spur (Fig. 5). The *truncus hyomandibularis* (principally composed of fibres from the VIIth cranial nerve) enters the hyomandibula through a dorsomedial foramen and passes down through its shaft to emerge from a ventrolateral foramen.

The posterior edge of the shaft is deeply grooved and accommodates the upper arm of the preoperculum. Dorsal to this groove the posterior edge is produced into a rounded condyle which articulates synchondrally with the operculum. A shallow vertical channel runs across the base of the posteroventral condyle. This channel houses the sensory canal between the preoperculum and pterotic canals.

The *metapterygoid* is widely separated from the hyomandibula (Fig. 5). Anteriorly, it is connected to the quadrate by a narrow cartilage interface and below the cartilage by a prominent dentate suture. The ventral edge contacts the dorsal edge of the symplectic, and the endopterygoid overlies the anterodorsal edge.

The *symplectic* is large (relative to the other suspensorial bones) and lies along the posteroventral arm of the quadrate (Fig. 5). The posterior end is cartilage-capped and connected by a fibrous band of tissue to the hyomandibula. Anteriorly, the symplectic tapers and lies in a recess in the posteromedial wall of the quadrate. The upper surface is produced into a thin lamina with an irregular dorsal edge.

The *quadrate* is fan-shaped (Fig. 5), its anteroventral angle bears a condyle which articulates, *via* a euarthroidal joint with the corresponding anguloarticular facet. The condyle is strengthened by the thickened ventral margin that is bound by connective tissue to the dorsal edge of the preoperculum. A deep recess in the medial face of the quadrate parallel to its ventral edge accommodates the anterior end of the symplectic. A further recess in the anteromedial wall, dorsal to the condyle, accommodates the large posterior ectopterygoid process.

The dorsal and posterodorsal edges of the quadrate are connected by a cartilaginous interface to the endopterygoid and metapterygoid, respectively.

The *endopterygoid* is boomerang-shaped (Fig. 5); its anterior arm lies in a shallow groove along the dorsal surface of the ectopterygoid. The short posterior arm is connected by its ventral edge to the quadrate and to the anterodorsal edge of the metapterygoid. The longer (anterior) arm extends below and beyond the anterodorsal connection of the ectopterygoid to the lateral ethmoid (discussed below; see Fig. 49).

The anterior edge of the *ectopterygoid* is sinusoidal (Fig. 5). A medial facet on the anterodorsal surface connects it directly with the lateral ethmoid. A groove extends for a short distance along the posterodorsal edge and accommodates the anterodorsal margin of the quadrate. Posteriorly, a horn-shaped process extends from the ectopterygoid to lie within a recess in the medial face of the quadrate.

The *palatine* is a long, flake-like element curved around the lateral face of the vomerine shaft (dermal and endochondral components cannot be distinguished in *M. mastacembelus*). A weak spur ascends dorsally to connect the palatine with the lateral ethmoid (Fig. 5). Posterior to the small spur the bone becomes dorsoventrally flattened beneath the anterior orbital region. There are no palatine teeth in this species.

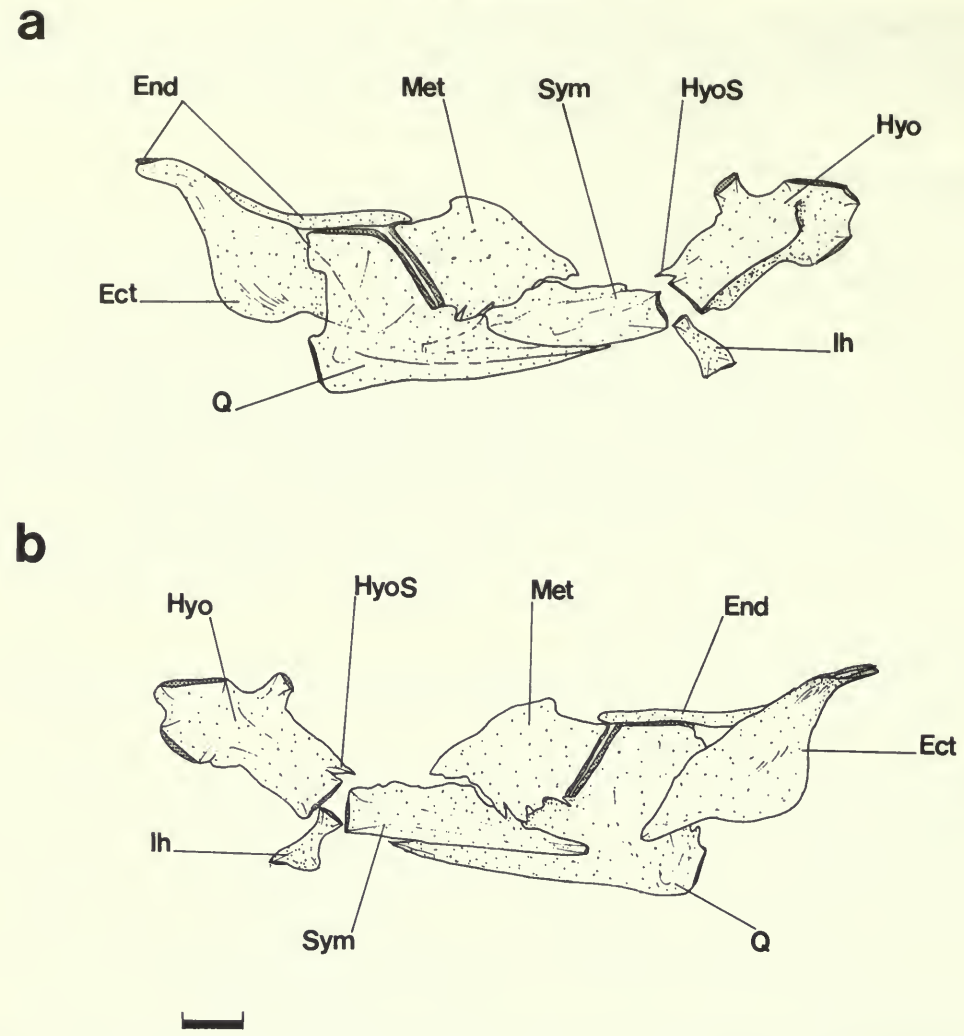


Fig. 5 *Mastacembelus mastacembelus,* left hyo-pterygoid arch in (a) lateral view, (b) medial view.

Opercular series

The *operculum* is characterised by a deeply concave dorsal edge (Fig. 6) which together with the weak, poorly ossified posterolateral flap is tightly sealed to the body-wall by the integument and underlying musculature (see p. 121). Thus, the branchial aperture lies below the suboperculum.

The ventral margin of the operculum overlaps the dorsal part of the suboperculum. A large facet on the anterodorsal edge articulates with a hyomandibular condyle and serves as a fulcrum for opercular dilatation, albeit only slight due to its restriction dorsally. A ridge crosses the lateral face and terminates in the dilatator process ventral to the opercular socket. The *levator operculi* muscle inserts along the dorsal surface of the ridge, and the *'musculus intraoperculi'* (which is unique to the mastacembeloids, see below p. 120) inserts along its ventral surface. The base of the opercular socket is pierced by a foramen which carries a ramus of the *truncus hyomandibularis* (*ramus opercularis superficialis facialis*). This nerve passes along a short enclosed canal to emerge on the anterolateral face of the operculum.

The *preoperculum* is L-shaped (Fig. 6). Its long, lower arm lies along the curved ventral

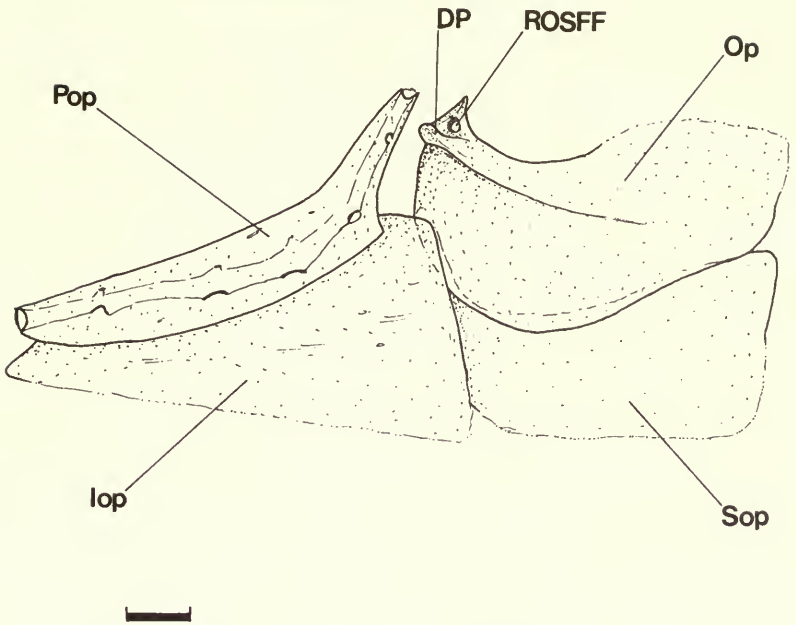


Fig. 6 Opercular series of *Mastacembelus mastacembelus*.

edge of the symplectic and quadrate, connecting them by its vertical arm to the hyomandibula. Anteriorly, the preoperculum is joined to the posterolateral wall of the angulo-articular by a short ligament. Preopercular spines are absent. The ventral edge overlaps the dorsolateral margin of the interoperculum, to which it is loosely joined by connective tissue. The upper arm of the preoperculum is narrow and lies along a deep lateral hyomandibular groove. The lateral face is pierced by 5 pores that open from its sensory canal (3 pores are present on the horizontal and 2 on the vertical limb).

The *interoperculum* is triangular, its broad posterolateral face bevelled anteriorly to a point just posterior to the mandible (Fig. 6); the interopercular ligament connects the anterior tip of the bone to the small retroarticular. Posteriorly, the interoperculum is sloped, dorsomedially, below the ventral edge of the preoperculum to which it is loosely joined by connective tissue.

The *suboperculum* is weak, its shorter, vertical arm hidden in lateral view by the anterior edge of the operculum and the posterior edge of the interoperculum (Fig. 6). The horizontal arm is broader than the vertical arm and the dorsolateral margin is overlapped by the ventral edge of the operculum. The ventral border is poorly ossified and, since it is not connected to the ventral body wall, it contributes to the posterior opening of the branchial chamber.

Hyoid and branchial arches

The *basihyal* is long and spatulate; a low ventral ridge runs along almost the entire length of the bone (Fig. 7). Posteriorly, the ridge lies in a groove along the anterior edge of the basibranchial 1 'keel' and forms a hinge joint.

The paired dorsal and ventral hypohyal bones are joined to basibranchial 1 by fibrous connective tissue. The *dorsal hypohyal* is small and caps the anterodorsal edge of the anterior ceratohyal, to which it is sutured by a number of tongue-like bony flanges (Fig. 7). The medial wall of the dorsal hypohyal is faceted and connects the anterolateral face of basibranchial 1.

Below this facet there is a large central foramen for passage of the hyoidean artery. Ventrally, the dorsal hypohyal is separated from the ventral hypohyal by a cartilaginous interface (Fig. 7).

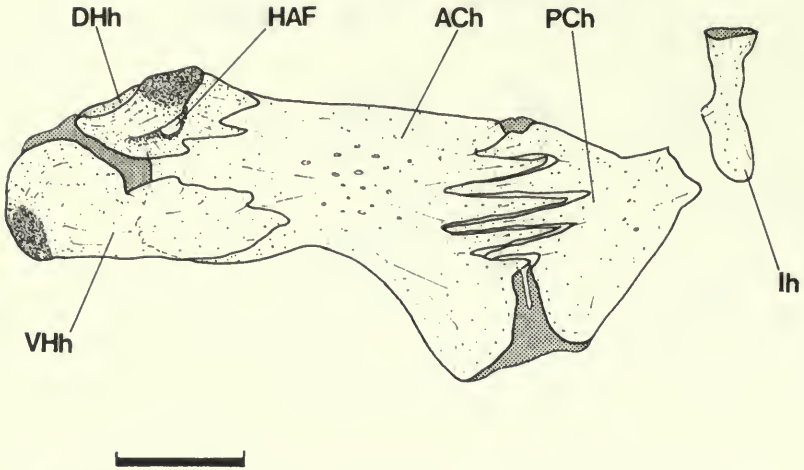


Fig. 7 *Mastacembelus mastacembelus,* right hyoid arch; medial aspect.

The *ventral hypohyal* is connected to the anterior ceratohyal by an interdigitating suture and a short band of cartilage (Fig. 7). Its anterior region is laterally compressed and a facet occurs on the medial face articulating with its partner in a median symphysis, anterior to the front edge of the keel on basibranchial 1. Below this facet is a shallow fossa, which accommodates the anterior end of a large ligament from the urohyal.

The *anterior ceratohyal* is compressed. Its posterior edge is joined to the anterior edge of the posterior ceratohyal by a large tripartite interdigitating suture, above and below which is a short connecting band of cartilage (Fig. 7).

Two branchiostegal rays (3rd and 4th) articulate with the lateral face of the anterior ceratohyal. The 5th branchiostegal is loosely connected to the medial face and the 6th (the weakest) attaches to the anteroventral margin of this bone. A 'berycoid' foramen (McAllister, 1968: 6) is absent.

The *posterior ceratohyal* is also compressed and is approximately triangular in outline (Fig. 7). The 1st and 2nd branchiostegal rays are loosely attached to its lateral face. The distal end is ligamentously connected to the ventral end of the interhyal.

The short, hour-glass shaped *interhyal* connects the posterior end of the hyoid arch (posterior ceratohyal) with the suspensorium, at a point between the symplectic and hyomandibula. The cartilaginous anterior and posterior ends of this bone have their long axes at right angles to each other.

The *urohyal* is extremely elongated and extends posteriorly from below basibranchial 1 to a point midway along ceratobranchial 5. The anterior end is bifurcated and from each head a large ligament extends forward to the ventral hypohyal. On its dorsal surface immediately posterior to its forked anterior end, is a small ascending process (directed posterodorsally), the tip of which lies below the keel on basibranchial I, and is loosely attached by connective tissue (Fig. 9). Posteriorly, the urohyal divides into four weakly ossified membranous prongs; a short dorsal and ventral prong with two large lateral prongs. The latter are subdivided into three small, posteriorly pointed processes (Fig. 9).

There are three ossified and a single cartilaginous basibranchial among the ventral gill arch elements.

Basibranchial 1 is cylindical with a deep ventral 'keel' which tapers to a knife-edge and lies partly below basibranchial 2 and the basihyal (Fig. 9). A round facet on the anterolateral surface lies across its junction with the basihyal, and articulates with the medial face of the dorsal hypohyal.

Basibranchial 2 is narrow-waisted (Fig. 8). The proximal end of hypobranchial 1 lies in the anterolateral, 'waisted' region. Posteroventrally, basibranchial 2 is united by fibrous tis-

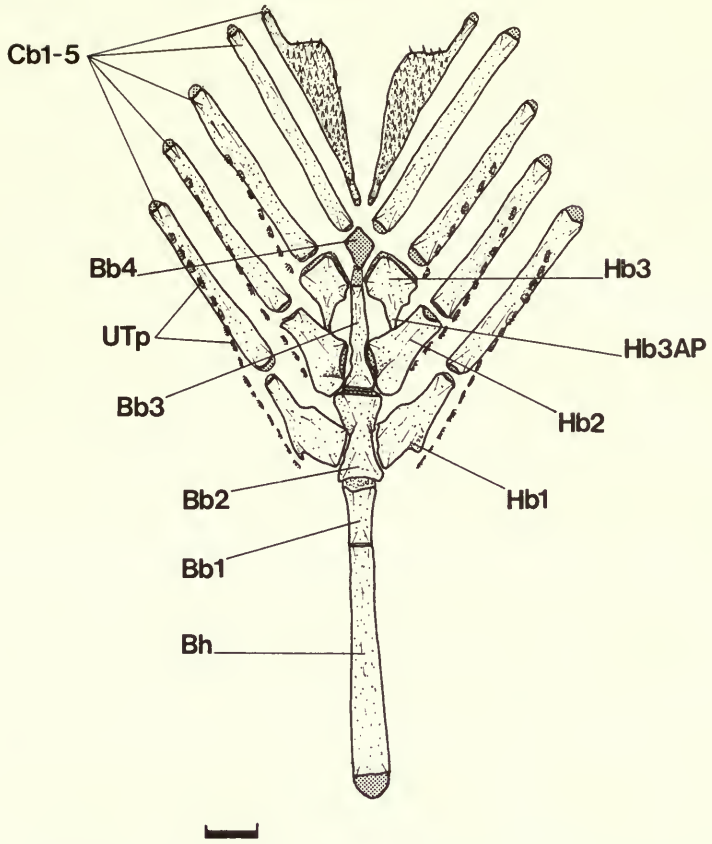


Fig. 8 *Mastacembelus mastacembelus,* lower gill arch elements; dorsal view.

sue to the anterior end of basibranchial 3. A prominent descending process extends from the median anteroventral surface and contacts the posterior edge of the 'keel' on basibranchial 1 (Fig. 9). A pair of descending processes also extend from each posterolateral corner of basibranchial 2. The tips of these processes are connected, by a pair of converging ligaments, to the posteroventral edge of the 'keel' on basibranchial 1 (the ventral aorta lies in the midline between these posteroventral processes).

Basibranchial 3 is long and relatively narrow; the medial end of hypobranchial 2 contacts the notched anterolateral wall. The posterior end is unossified and forms a rod-like length of cartilage capable of sliding below basibranchial 4 when the branchial arches contract (Fig. 8).

Basibranchial 4 is a rhomboid, cartilaginous element (Fig. 8). Its anterolateral face contacts the posteromedial edge of hypobranchial 3, and its posterolateral edges the ends of the 4th and 5th ceratobranchials.

Hypobranchials 1 & 2 each have a broad proximal (anteromedial) face faceted for articulation with their corresponding basibranchial elements. Hypobranchial 2 is also connected, by a medial flange, to the posterolateral descending process on basibranchial 2.

Hypobranchial 3 is characterised by a large anteroventral process extending forward below the 2nd hypobranchial. The anterior tip of this process is ligamentously attached to the posterior descending process on basibranchial 2; the ligament merges in the midline with its opposite number to produce a wide, ventral sheet of collagenous tissue. The ventral aorta runs along the dorsal surface of this medial aponeurosis, between it and the basibranchial elements.

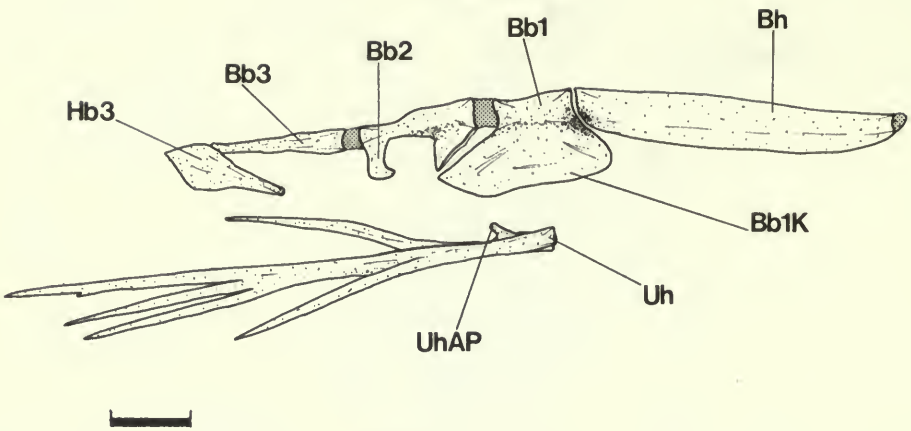


Fig. 9 *Mastacembelus mastacembelus*, basihyal and branchial bones in lateral view, right side.

The posterior end of each hypobranchial is connected by fibrous tissue to its corresponding ceratobranchial. Small, irregularly positioned dermal toothpatches are supported along the anterior margin of hypobranchial 1 and 2. No toothplate is associated with the dorsal surface of hypobranchial 3.

Ceratobranchials 1–5 are rod-like elements; with the exception of the 5th, are all essentially alike. The distal ends of ceratobranchials 1–4 are each joined by connective tissue to a corresponding epibranchial bone. Along the ventral face of ceratobranchials 1–4 is a hollow channel that accommodates the efferent blood vessels and the bases of the gill filaments. Numerous small, round, dermal toothpatches are supported along the anterior face of ceratobranchials 1–4.

The 5th ceratobranchial bears a large fused toothplate ('lower pharyngeal jaw'). This toothplate is expanded posteromedially, but does not contact its partner in the midline. The medial edge of the expanded toothplates and the posteromedial margin of the bone are joined to the oesophagus. The toothplate bears acrodont caniniform teeth graded in size, with the largest along the medial edge. The posterior end of ceratobranchial 5 forms a relatively short 'muscular process' (Liem, 1974). A broad sheet of fibrous tissue connects the posterolateral edge to the lateral face of the cleithrum.

The dorsal gill arch elements lie posterior to the cranium.

Epibranchials 1 and 2 are each characterised by wide anterior edges; a round dermal toothplate is supported on the anteroventral face of each (Fig. 10).

Epibranchials 3 and 4 both bear an ascending uncinate process. The dorsal tips of these processes are connected by a short collagenous strand of tissue.

Apart from a short lateral region, the dorsal edge of each epibranchial is free of gill filaments.

Pharyngobranchials 2 and 3 are the only ossified pharyngobranchial (infrapharyngobranchial) elements present. The posterior end of pharyngobranchial 2 is attached by a collagenous strand to the medial end of epibranchial 2. This collagenous strand is also connected to the tip of a short process on the lateral margin of pharyngobranchial 3. Pharyngobranchial 3 extends anteriorly from this process to lie parallel with the anterior end of pharynobranchial 2. A collagenous strand of tissue connects their anterior tips with the medial end of epibranchial 1 (Fig. 10). There is no trace of an interarcual cartilage (Travers, 1981) between epibranchial 1 and pharyngobranchial 2.

The posterior end of pharyngobranchial 3 is broad and connected to the medial end of epibranchial 3.

A small cartilaginous element lying posterior to pharyngobranchial 3 (between it and the medial end of epibranchial 4) is interpreted as a cartilaginous 4th pharyngobranchial. The

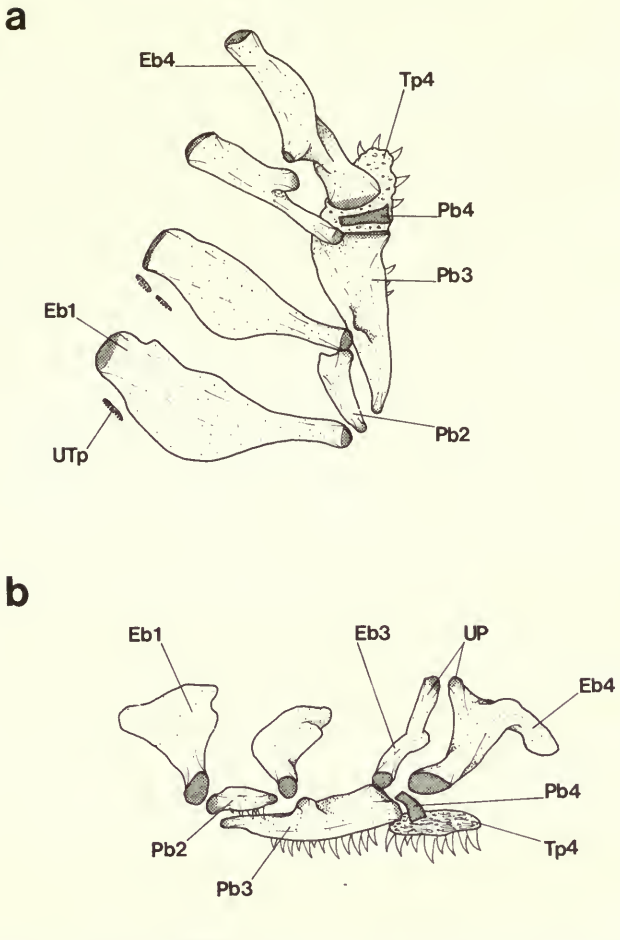


Fig. 10 *Mastacembelus mastacembelus,* right upper gill arch elements in (a) dorsal view, (b) medial view.

largest toothplate of the dorsal gill arch elements is fused to the ventral face of pharyngobranchial 3. A smaller toothplate is fused to the ventral face of pharyngobranchial 2. A further toothplate lies ventral to the cartilaginous pharyngobranchial 4.

The toothplates on the pharyngobranchial bones, together with the free 4th pharyngobranchial toothplate, constitute the 'upper pharyngeal jaws'. The dentition of these elements is similar to that found on ceratobranchial 5 which they oppose.

There are no *gill rakers* on the branchial arches.

Pectoral girdle

The pectoral girdle lacks a bony connection to the neurocranium and lies posterior to it adjacent to the 3rd and 4th abdominal vertebrae.

The thin *supracleithrum* is relatively long and narrow (Fig. 11). The ventral end overlaps the dorsolateral wall of the cleithrum to which it is loosely attached. A portion of the postcranial sensory canal system passes longitudinally through its dorsal tip.

The *cleithrum* is the largest bone of the pectoral girdle. It has a vertical dorsolateral shaft and a ventral limb which curves anteromedially to contact its partner in a median symphysis. The scapula and coracoid lie just distal to a trough-like region in the lateral face (Fig. 11).

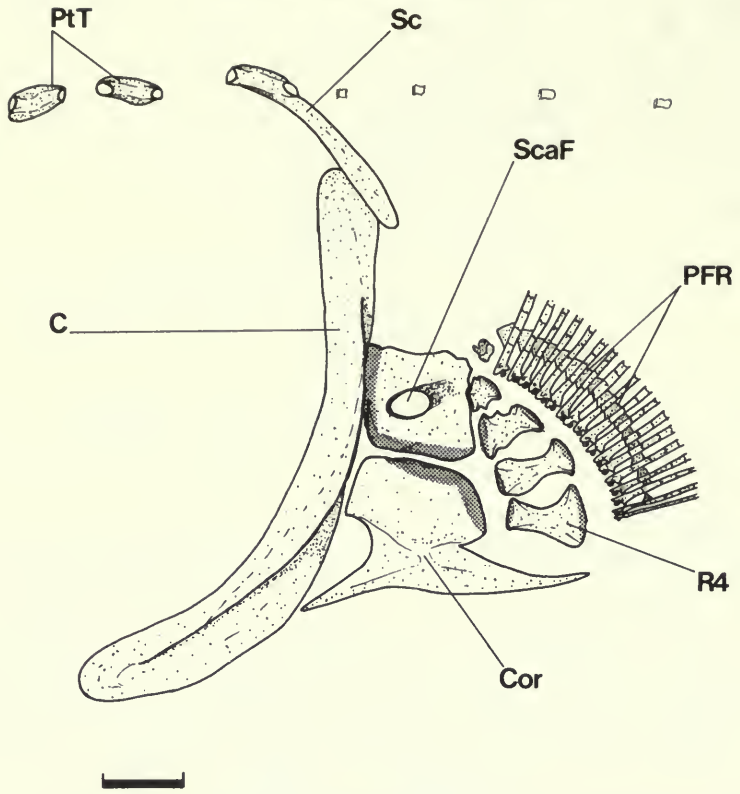


Fig. 11 *Mastacembelus mastacembelus,* lateral view of pectoral girdle; left side, with two post-temporal tubules.

Baudelot's ligament extends between the basicranium and dorsomedial face of the cleithrum and the ventromedial face of the supracleithrum.

The *scapula* is almost square in lateral outline. A large foramen pierces its anterolateral face; the nerve trunk to the pectoral fin rays passes through this opening. The cartilaginous anterior edge lies within the dorsal region of the cleithral trough. The posterior edge supports the 1st and 2nd radials and dorsal to these a slight posterior projection of the scapula articulates directly with the base of the primary fin ray (Fig. 11). The scapula and coracoid are separated by a narrow cartilage interface.

The *coracoid* is a narrow-waisted, flat bone; the lower region drawn out both anteriorly and posteriorly into pointed processes. The posterior process extends to a point below the posterior edge of the radials. The dorsal cartilage interface extends along the posterodorsal edge and supports the 3rd and 4th radials.

The four *radials* (actinosts) are short, spool-like, independent elements; the smallest lying dorsally (1st). The ends of each radial are cartilaginous and form a shallow facet for articulation anteriorly with the scapula and coracoid (as described above) and posteriorly with the base of each fin ray.

The pectoral fin has 22 segmented *fin rays*; each composed of independent halves and branched distally. The innermost halfrays (posterior) each have a ventral proximal process that overlaps the lower neighbouring halfray (Fig. 11). Distal to this process is a 2nd triangular flange that overlaps the upper neighbouring element. The outer (anterior) halfrays also have a ventral bony lip overlapping the lower neighbouring element. Fin movement results in a complex interlocking of these flanges.

Vertebral column

The total vertebral count is 86, *viz.*, 38 abdominal (precaudal vertebrae), 47 caudal and the fused ural and first preural centra. Following the method of Greenwood (1976: 65) the first caudal vertebra is identified as that with which the first anal pterygiophore articulates.

The first four *abdominal vertebrae* are the most distinctive of the entire series (Fig. 12). Their broad neural arches are pierced by numerous perforations. The anterior half of the 1st centrum is rounded to form a hemispherical condyle. This condyle articulates with the tripartite occipital socket in a 'ball and socket' joint. The first neural arch contains a distinctly large foramen just above its point of fusion with the centrum.

The neural spines of the first four abdominal vertebrae are laterally compressed and elongated. The 1st abdominal vertebra has the largest neural spine (4–5 times wider than the spine on the 5th vertebra); the anterior and posterior edges are approximately parallel and the dorsal edge produced into 3 separate peaks. The 2nd, 3rd and 4th neural spines have 2 dorsal peak-like processes, and the posterior edge of the 2nd is deeply notched. Pre- and postzygapophyses are well developed on all but the 1st abdominal vertebra.

Along the abdominal vertebrae there are a total of 3 pairs of epicentral and 1 pair of epipleural ribs. The *epicentral ribs* occur on the 1st to 4th vertebrae and *epipleural ribs* on the 4th only. The 1st epicentral is lodged in a recess on the lateral wall of the 1st centrum; all other epicentral ribs are supported by their anterior ends lying in a shallow channel along the dorsal surface of the lateral parapophyses.

Lateral parapophyses are present on all abdominal vertebrae except the 1st, and decrease in size posteriorly.

The *Pleural ribs* are all supported in a groove along a ventral arm of the lateral parapophyses (Fig. 12).

By the 10th abdominal vertebra the lateral parapophysis is reduced to a low notch and the ventral arm developed into a prominent, ventromedially curved parapopyhysis that sup-

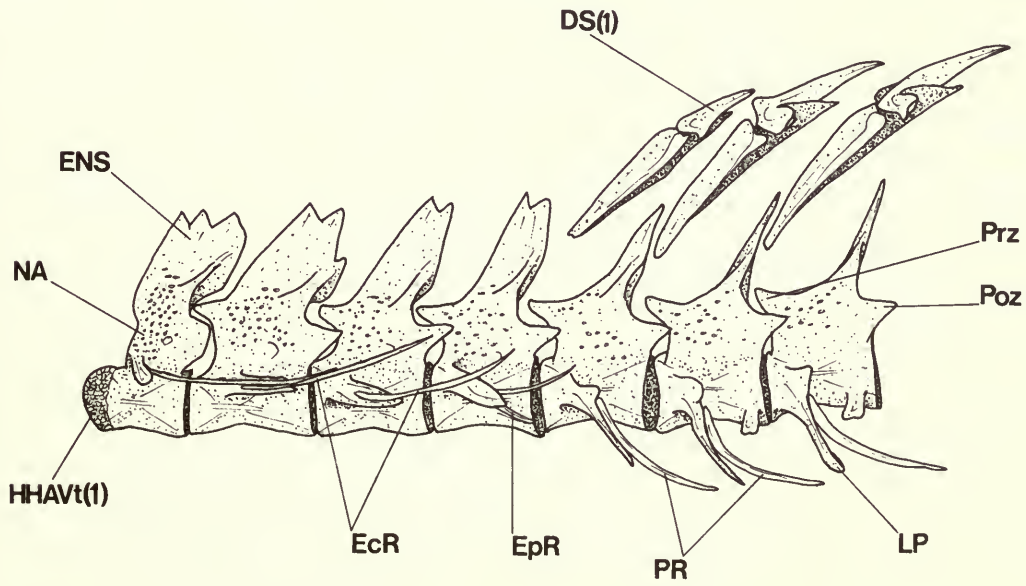


Fig. 12 *Mastacembelus mastacembelus,* anterior abdominal vertebrae with first three dorsal spines; lateral aspect, left side.

ports a large (posteriorly tapered) pleural rib. By the 13th abdominal vertebra the pleural ribs are no longer medially curved. On the 6th and all succeeding abdominal vertebrae there is also a short descending process on the ventral face of the centrum (posterior half).

The abdominal centra are characterised by their asymmetry as the posterior region of each appears to have been drawn out. However, the asymmetry of the centra is gradually lost posteriorly and the last 10 *caudal vertebrae* are symmetrical.

The parapophyses on the 1st caudal vertebra (Fig. 13) are connected in the midline by a short band of fibrous tissue (forming a rudimentary haemal arch). These parapophyses are also branched and support the massive pterygiophore carrying the 1st and 2nd anal spines.

Dorsal and anal fins

There is a total of 35 *dorsal spines* and supporting pterygiophores associated with the 4th to 38th abdominal vertebrae (excluding the 31st and 35th) and the 2nd and 3rd caudal vertebrae. The spines are relatively short, stout structures, curved posterodorsally. Anteriorly, each spine is held in position by the distal end of the supporting pterygiophores, which are fused and form a stout bone that tapers to a point anteroventrally. The distal region of these pterygiophores bears a pair of prominent hooks that lie (laterally) on either side of the spine and hold its base firmly in position (Fig. 13). The proximal end of each spine bears a pair of small anterolateral processes around which the distal pterygiophore is hooked; a pair of lateral ridges present along the pterygiophore, separate the erector from the depressor

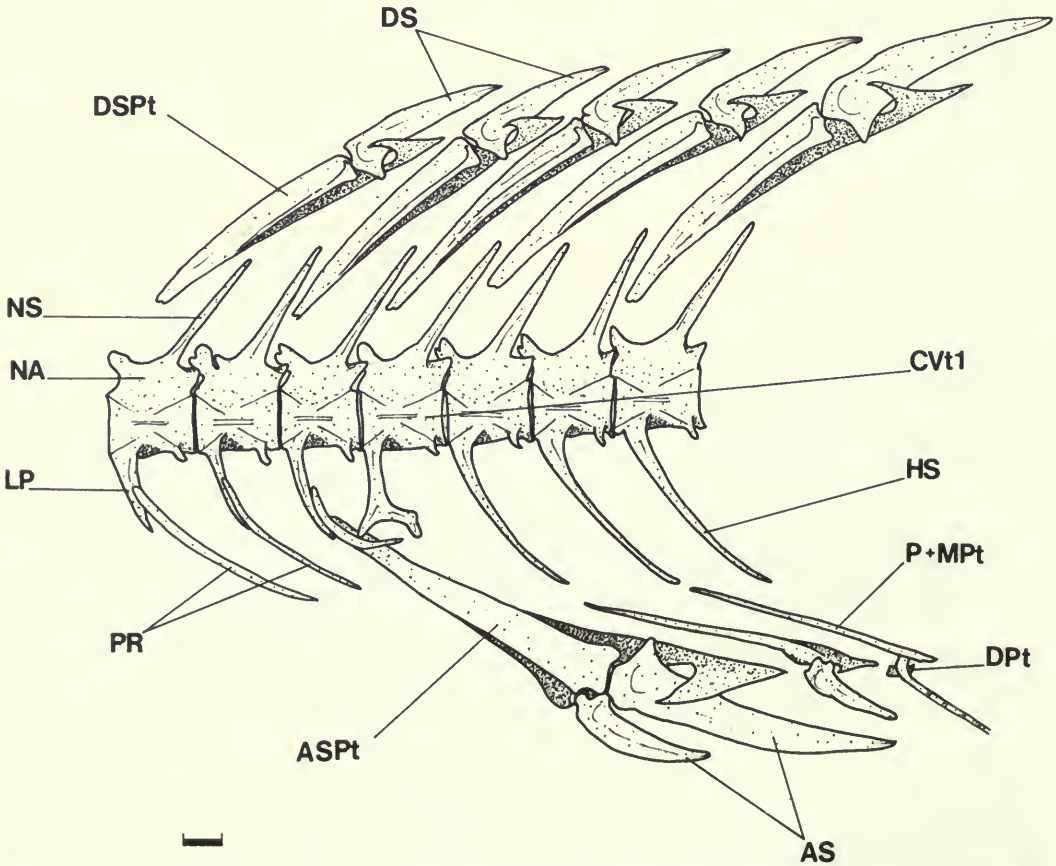


Fig. 13 *Mastacembelus mastacembelus,* abdominal/caudal vertebral junction and associated dorsal and anal spines; lateral aspect, left side.

muscles. A ligament passes from the base of the spine along the anterior edge of the supporting pterygiophore and contributes to the articulation between these elements.

There are 3 *anal spines* (Fig. 13); all are similar in morphology to the dorsal spines except that the 1st and 2nd share a massive pterygiophore. This pterygiophore is supported by the rudimentary haemal arch of the 1st caudal vertebra.

The non-spinous *dorsal* and *anal fins* are composed of 70–73 and 74–78 segmented rays respectively. They extend from the posterior spinous rays to the dorsal and ventral edge of the caudal fin. Each ray is supported by a pterygiophore system composed of 3 elements. On the whole, most neural and haemal spines are associated with 2 pterygiophores; hence each supports 2 fin rays (by the connection of a proximal pterygiophore to the anterior and posterior edges of each neural and haemal spine).

The *proximal pterygiophore* is a long, ventrally pointed bone much smaller and weaker in comparison with its spine supporting counterpart. The distal end is fused to a cone-shaped medial pterygiophore, the two forming a single unit (Fig. 13). The dorsal surface of the *medial pterygiophore* is flat and the small, independent distal pterygiophore of the preceeding fin ray articulates with it. The posterior end of the medial pterygiophore is collagenously joined to the distal pterygiophore of the same ray.

The *distal pterygiophore* is a small saddle-shaped independent structure, composed of separate halves. It lies between the base of the fin ray and the supporting medial pterygiophore element.

Caudal fin

The caudal fin rays lie posterior to the last ray of the dorsal and anal fins, to which they are joined by a thin membrane.

The *hypural* bones fan out from the fused ural and first preural centra and are composed of 4 relatively large, autogenous elements (2 above and 2 below the lateral line), and an extremely small splint of bone along the dorsal edge of the upper hypural (Fig. 14). Ventral to these lies an independent *parhypural.* A large vascular canal passes through the head of this bone (Fig. 14).

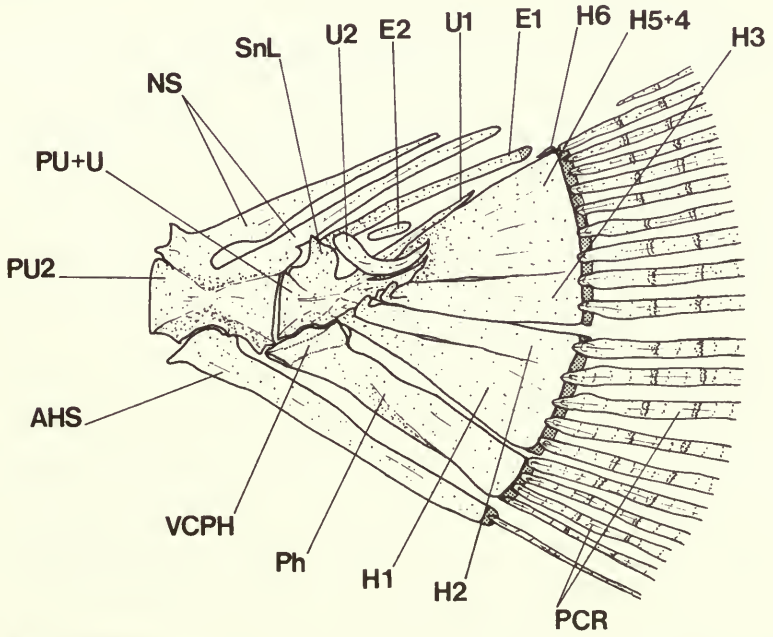


Fig. 14 *Mastacembelus mastacembelus*, caudal fin skeleton; lateral aspect, left side.

A *uroneural* (1) is fused along the dorsal edge of the fused ural and preural vertebra and is tapered to a fine point posteriorly. A second, sickle-shaped uroneural bone (2) lies lateral to the first and the base of the dorsal hypural.

A long *epural* extends posteriorly from the reduced neural arch on the fused ural and preural centra to the anterior region of the fin rays. Between this long epural and the fused ural and preural vertebra is a second, smaller epural element.

The 2nd preural vertebra bears an autogenous haemal arch from a deep V-shaped notch in the lateral wall of the centrum. The haemal spine on this arch is long and directly supports the ventral caudal fin ray. The neural arch is large and fused to the centrum. Two spines extend from this arch and may indicate that intervertebral fusion has occurred. These neural spines are long but do not contribute to the support of caudal fin rays.

There are 19 segmented, unbranched caudal fin rays (9 forming the upper lobe and 10 the lower lobe of the caudal fin).

Squamation

Small *cycloid scales* cover the body and head, except for its dorsal surface, i.e. the nasals, frontals & parietals.

Osteology of *Chaudhuria caudata*

This description is based on three specimens (see Table 3). Two individuals (38 mm. and 42 mm. standard length) from the collections at the BM(NH) are alizarin stained only. A third specimen (on loan from the MCZ) was double stained and is 43 mm. long. In this alizarin/alcian blue transparency numerous mature eggs (approx. 30) are visible in the posterior region of the body cavity, indicating that specimens of *Chaudhuria* at this size are adult.

Neurocranium

Ethmovomerine region

The *supraethmoid* is a particularly elongate bone; it consists of a laterally compressed region separating the olfactory sacs, and a short posterodorsal process lying between the anterior tips of the frontal (Fig. 15ai). The anterodorsal edge is indented and supports a relatively large tapered rostral cartilage. The anterior tip is divided into two short, blunt processes. Ventrally this region is fused to the anterodorsal edge of the vomer; posteroventrally it remains cartilaginous and extends along the anterodorsal surface of the parasphenoid and into the orbital cavity as a septal cartilage.

The *vomer* is developed anteriorly into a facet which extends around the tip of the bone. The anterolateral region of this facet articulates with the medial face of the ascending process of the premaxilla. The vomerine shaft lies in a ventral groove in the parasphenoid and extends posteriorly to a point adjacent to the anterior end of the prootic.

Each *lateral ethmoid* is a vertical, plate-like bone pierced by a large central opening. The medial edge contacts its partner in the midline dorsal to a cartilaginous septal region of the supraethmoid. Short anterior and posterior processes extend from the dorsal edge of the lateral ethmoid and are covered by the nasal and frontal respectively. The narrow ventrolateral face is joined syndesmotically to the posterodorsal tip of the 1st infraorbital.

The flattened *nasal* slopes ventrolaterally and covers the olfactory cavity; it is poorly ossified (especially anteriorly). The medial edge is loosely connected to the dorsal margin of the supraethmoid, and the lateral edge to the 1st infraorbital bone (Fig. 15aiii). Posteriorly it extends as a flattened projection above the lateral ethmoid and anterior surface of the frontal.

Orbital region

The *pterosphenoid* and *basisphenoid* are absent. The *parasphenoid* has a long, narrow

anterior process which terminates ventral to the lateral ethmoids (Fig. 15aii). It lacks a distinct ascending arm and has only a low lateral wall contacting the posteroventral edge of the prootic; it is unattached to any other bone. Posteriorly, the lateral wall is reduced to a shaft ventral to the median connection between the prootic bones. From this region the parasphenoid is divided into a pair of long, needle-like processes which extend to the posteroventral edge of the basioccipital. A low ventral ridge on the basioccipital lies between these processes. Adjacent to the lateral commissure the dorsal margin of the parasphenoid is notched for passage of the internal carotid artery.

The *1st infraorbital* bone is the only poorly ossified element of the infraorbital series present. It tapers anteriorly and contacts the ventral edge of the nasal and dorsal surface of the maxilla (Fig. 16a). The posterodorsal edge is indented and surrounds the ventral rim of the posterior olfactory opening. The posterior edge of this opening is formed by an ascending posterodorsal process on the 1st infraorbital. The medial tip of this process articulates synchondrally with the lateral ethmoid.

Otic region

The *prootic* is a particularly long bone and has a wide, tapered, anterior process extending to the orbital cavity. (Fig. 15ai). The dorsal connection with the sphenotic is interrupted by the single foramen in the pars jugularis. A slender lateral commissure arches across the centre of this foramen. Anterior to the trigeminofacialis chamber the prootic tapers into a long rostrodorsally directed process. Its dorsolateral face is pierced by a pair of round foramina which open into a medial groove along the anteromedial face of the process, and extend to its tip.

A shallow fossa in the posterodorsal margin of the prootic combines with a similar one in the sphenotic to accommodate the anterior hyomandibular condyle. Posteriorly, the prootic borders the pterotic, exoccipital and basioccipital bones and houses the anterior third of the sacculus.

The *sphenotic* lies between the dorsal edge of the prootic and the dorsolateral edge of the frontal. It has a long anterior projection extending into the orbital cavity, and terminates as a broad, blunt process, slightly posterior to the tip of the prootic anterior process (Fig. 15ai). The ventral edge forms the anterodorsal rim of the single foramen in the pars jugularis. A postorbital process is absent. The posterior edge borders the pterotic, and a posterodorsal process extends medially below the parietal to connect, synchondrally, the tip of a process apparently originating from the ventral surface of the supraoccipital.

The *pterotic* is an inflated bone, due to a medial cavern that encloses the horizontal semicircular canal, with a grooved ventral surface that accommodates the posterior hyomandibular condyle (Fig. 15aii). The dorsal edge is overlapped by the dorsolateral margin of the parietal. Ventrally it contacts the prootic and exoccipital and forms with these bones a relatively deep lateral recess. The posttemporal fossa is absent and posteriorly the pterotic borders the epioccipital.

The *epioccipital* lies between the exoccipital and pterotic and dorsally contacts the posterolateral edge of the supraoccipital and posterior edge of the parietal.

The inner face of the epioccipital houses the posterior semicircular canal which causes its relatively wide dorsolateral face to be somewhat bullate.

The *exoccipital* has a perforated dorsal surface which is prevented from contacting its partner in the midline by a posterior extension of the supraoccipital. The posterolateral face of the bone has three major foramina, *viz* those of the glossopharyngeus, occipitospinal and vagus nerves. This region is curved ventromedially and contacts its partner in the midline dorsal to the basioccipital.

Below their median connections the ventral surface of each exoccipital is developed into a slightly concave, deltoid facet. These facets, with a similar one from the basioccipital, form the tripartite occipital facet, a concave socket that articulates with the rounded anterior end of the 1st abdominal centrum (Fig. 21aii). The ventral region of the exoccipital bears a small

process which is directed posteriorly and extends beyond the posteroventral edge of the basioccipital.

The *basioccipital* is large, relative to the size of the other basicranial bones, and contacts the exoccipital and prootic (Fig. 15aii). The long ventral processes on the parasphenoid pass across its ventral surface on either side of a low longitudinal ridge. The posterodorsal surface is faceted and contributes to the tripartite occipital socket.

The *supraoccipital* is the major element in the roof of the basicranium (Fig. 15aiii). It is a flattened bone that is transversely convex and bounded on either side by the posterior

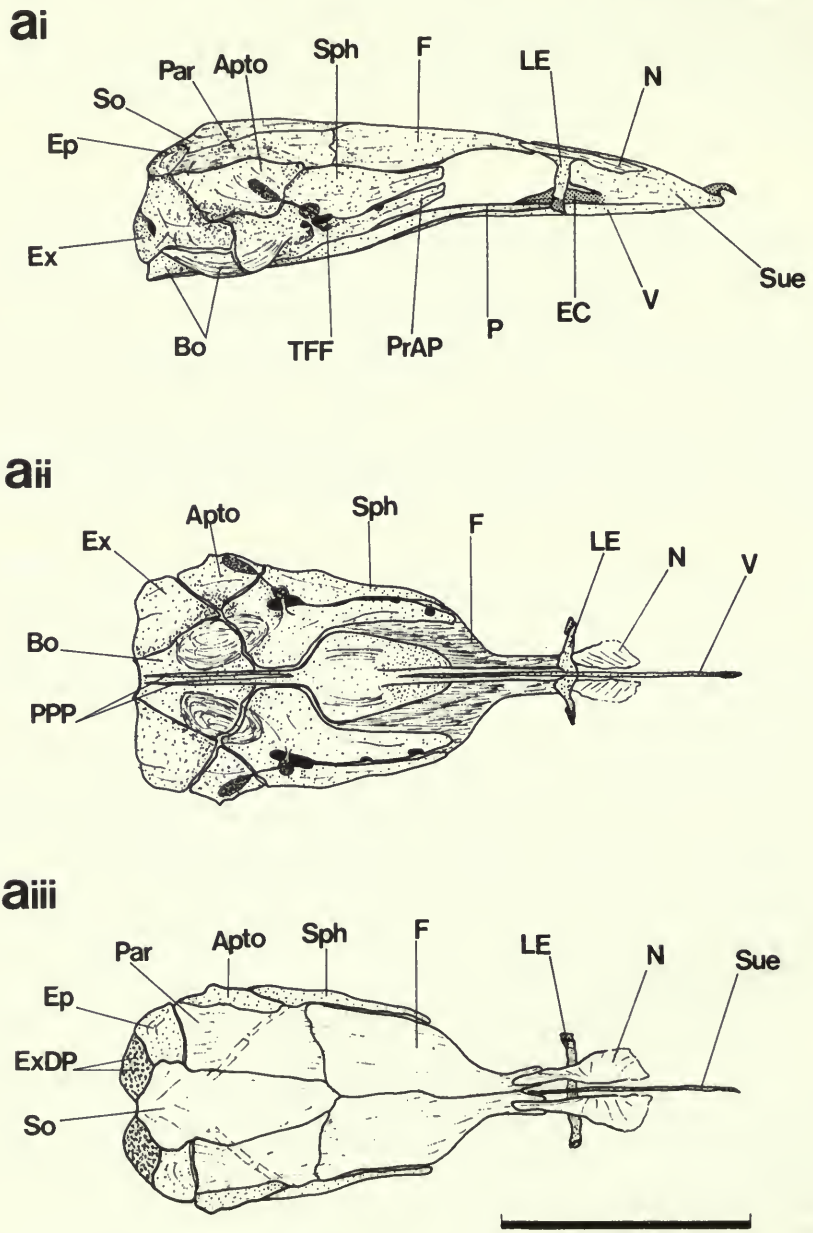
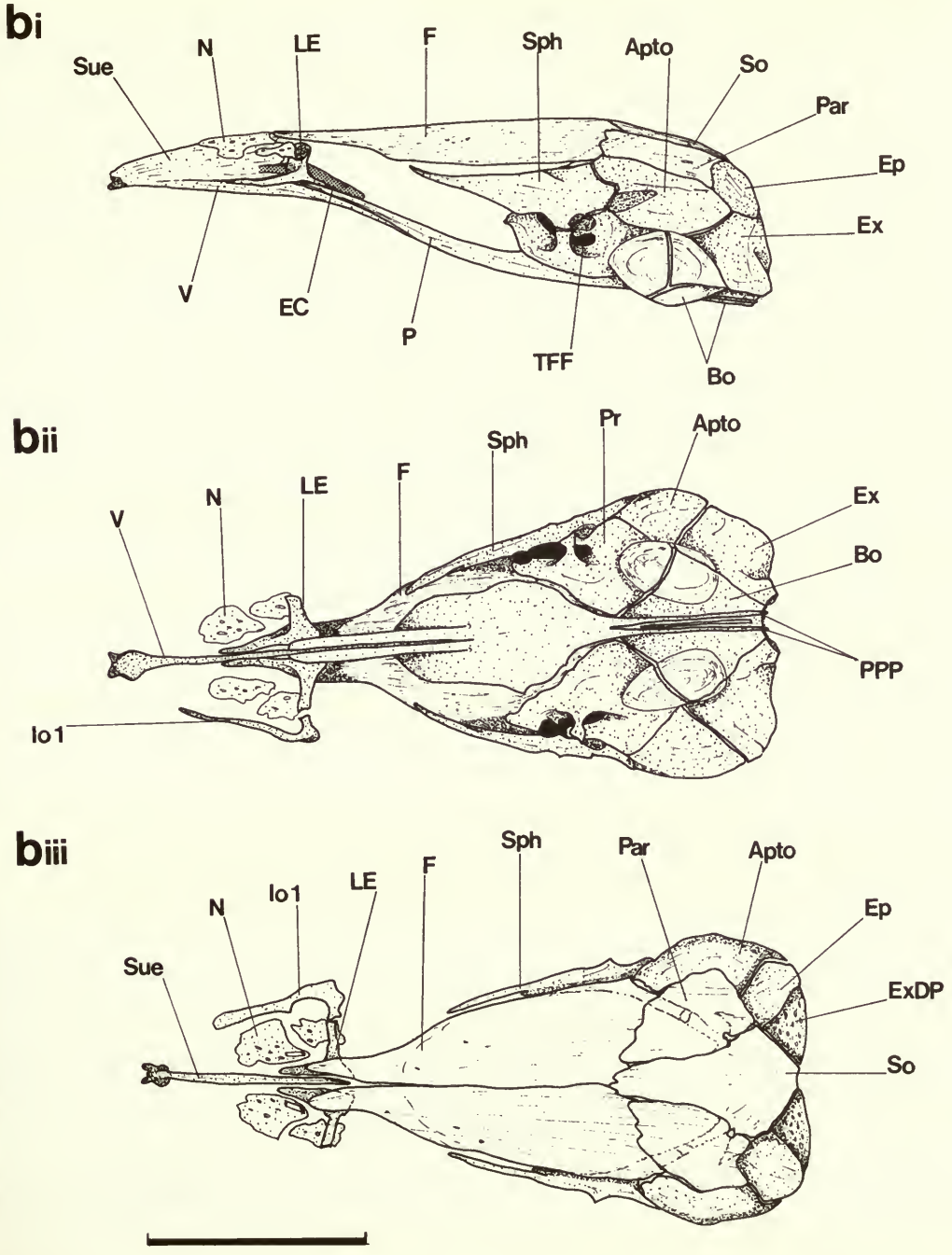


Fig. 15 Neurocranium in (a) *Chaudhuria caudata,* and (b) *Pillaia indica*: right lateral view (ai & bi), ventral view (aii & bii) and dorsal view (aiii & biii).

portion of the frontals, the parietals, epioccipitals and the dorsomedial edge of the exoccipitals. However, none of these surrounding bones overlaps the supraoccipital margin. Its posterior edge contributes to the rim of the foramen magnum.

There is no sign of the *extrascapula* (lateral or medial) or the *posttemporal* bones.

The flattened dorsal surface of the *frontal* narrows anteriorly as a short process that terminates below the posterior end of the nasal (Fig. 15aiii). Posteriorly, the frontal is long and curved ventrolaterally. A descending lamina is absent.



The *parietal* has a flattened, unsculptured dorsal surface that is relatively broad compared with the other roofing bones (Fig. 15aiii). It lacks a posterolateral flange and is surrounded by the supraoccipital, frontal, pterotic and epioccipital bones. A notch along its posteromedial edge forms, with the margin of the supraoccipital, a small dorsal opening.

There is no sign of the *cephalic sensory canal system* in any neurocranial bones. The somatic component passes through the tip of the supracleithrum and appears to terminate just posterior to the cranium.

Jaws

The upper jaw in *Chaudhuria,* based on Annandale's (1918) original description, was assumed by Yazdani (1978: 284) to consist of a single bone; however, this is not the case.

The *premaxilla* is a long, narrow, weakly curved bone, and has a low stump-like ascending process on its anterodorsal surface (Fig. 16a). The ventral surface has a narrow alveolar surface that bears 2 rows of long, weak villiform teeth (decreasing in size posteriorly).

The *maxilla* is a relatively large bone (compared with the size of the premaxilla; Fig. 16a). Its anterior end extends to the posterior edge of the premaxillary symphysis and is connected to the premaxilla ascending process and lateral facet on the head of the vomer. Posteriorly the maxilla overlies the lateral face of the coronoid process on the dentary.

The *dentary* is relatively short. Its symphysis lies in the vertical posterior to the premaxillary symphysis. A prominent symphysial process descends from the anteroventral edge. Posteriorly, the dentary divides into an upper coronoid and lower ventral arm (Fig. 16a). The coronoid region is developed into a tall, narrow process. The dorsal surface anterior to the coronoid process is alveolate and bears 3 rows of villiform teeth, decreasing in number and size posteriorly. The ventral arm of the dentary extends posteriorly as a long pointed process lying below the margin of the anguloarticular. From the ventral edge of this process a further short posteromedially directed process may develop. The region between these processes may be bridged by partly ossified tissue.

The *anguloarticular* is long and pointed (Fig. 16a). Its dorsal edge is straight, apart from a low projection on the anterior edge of the posterodorsal facet. Meckel's cartilage lies along the medial face, and passes into the dentary.

The *retroarticular* is a small, L-shaped bone (its shorter horizontal limb extending anteriorly). The dorsal surface of the vertical limb articulates synchondrally with the posteromedial face of the anguloarticular facet (Fig. 16a). The interopercular ligament is connected to the posterior edge.

The *coronomeckelian* is a short rod of bone that lies on the posterodorsal surface of Meckel's cartilage but does not protrude above the dorsal edge of the anguloarticular (Fig. 16a). The anterior end of the tendon from part A_3 of the *adductor mandibulae* inserts on the coronomeckelian.

Hyopalatine arch

The *hyomandibula* is a short, stout bone, its dorsal surface produced into two condyles which articulate with the lateral face of the neurocranium, and its posterodorsal edge produced into a third condyle which articulates with the operculum (Fig. 17a). The descending hyomandibular shaft is short and is joined to the symplectic and interhyal medial to the preoperculum. A wide flange anterolateral to the shaft is connected anteriorly to the metapterygoid and ventrally to the posterodorsal edge of the symplectic. A large foramen for the *truncus hyomandibularis* pierces the lateral wall of the hyomandibula, ventral to its anterior condyle.

The *symplectic* is a rod-like bone without dorsal lamina, and does not extend forward to the quadrate (Fig. 17a).

Its dorsal edge is connected to the ventral edge of the metapterygoid, and ventrally it lies along the lower limb of the quadrate, passing posteriorly on the medial aspect of the preoperculum.

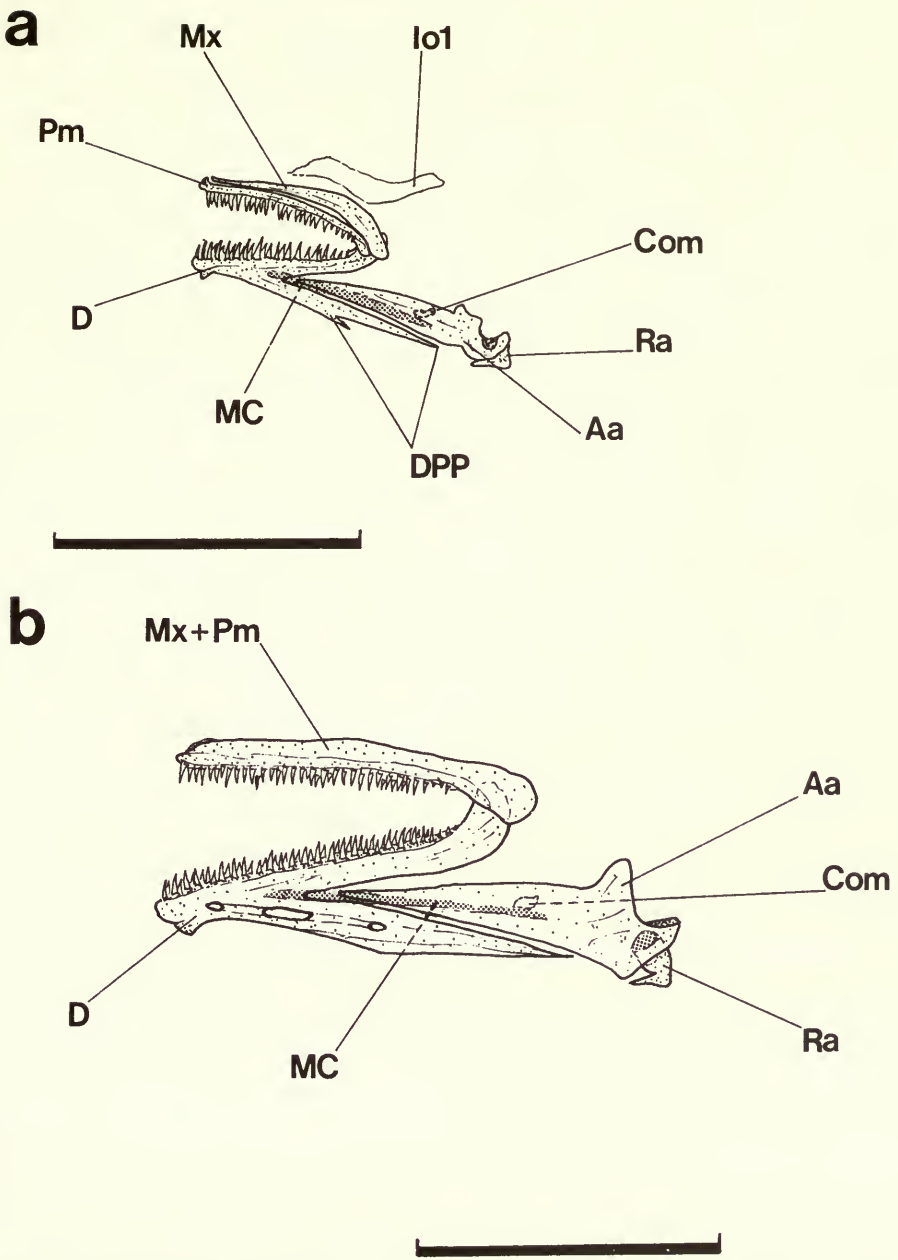


Fig. 16 Upper and lower jaw bones in (a) *Chaudhuria caudata* and (b) *Pillaia indica;* lateral view, left side.

The *metapterygoid* lies close to the anterior edge of the hyomandibula. Its anterior edge is connected by a cartilaginous interface with the quadrate. The anterodorsal corner has a slight projection that overlies the dorsal edge of the quadrate.

The *quadrate* is large in comparison with the other suspensorial bones. Its anterior edge is notched and ventrally forms a stout condyle which articulates with the anguloarticular facet. This condyle is strengthened by the thickened ventral region of the quadrate.

An *endopterygoid* is absent.

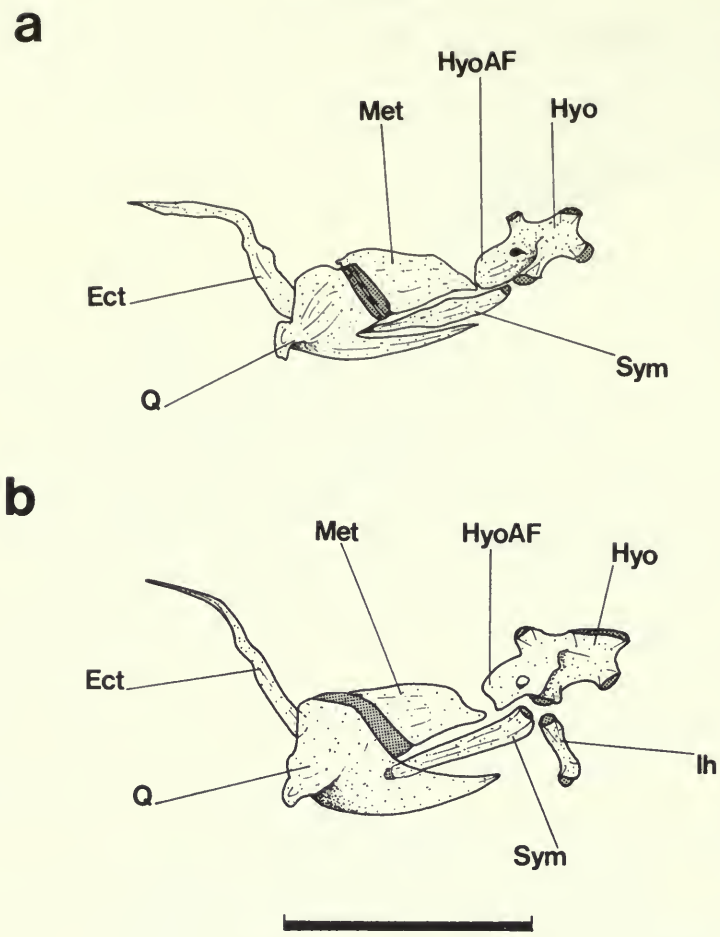


Fig. 17 Hyopalatine arch, in (a) *Chaudhuria caudata* and (b) *Pillaia indica*; lateral view, left side.

The *ectopterygoid* is particularly long with a relatively narrow lateral face whose posterior region lies medial to the anterior edge of the quadrate (Fig. 17a).

The anterior limb is curved medially (ventral to the lateral ethmoid) and has its medial face connected to the vomerine shaft. This is the anterior suspensorial articulation with the neurocranium as there is no connection between the ectopterygoid and lateral ethmoid.

The *palatine* is absent.

Opercular series

The *preoperculum* is crescentic, lacking distinct vertical and horizontal arms; the lateral face is wide (Fig. 18a). Dorsally, it is tucked within a deep groove on the lateral face of the hyomandibula.

The *interoperculum* is connected ligamentously to the retroarticular and has a poorly ossified ventral margin.

The *suboperculum* has a thin dorsal arm that ascends between the interoperculum and operculum, apart from this arm it is poorly ossified.

The *operculum* is developed anterodorsally into a prominent concave facet for articulation with the posterior hyomandibular condyle (Fig. 18a). The ridge on its lateral face extends from the base of the facet and forms a distinct dilatator process. The dorsal edge of the operculum is notched and its posteroventral margin is poorly ossified.

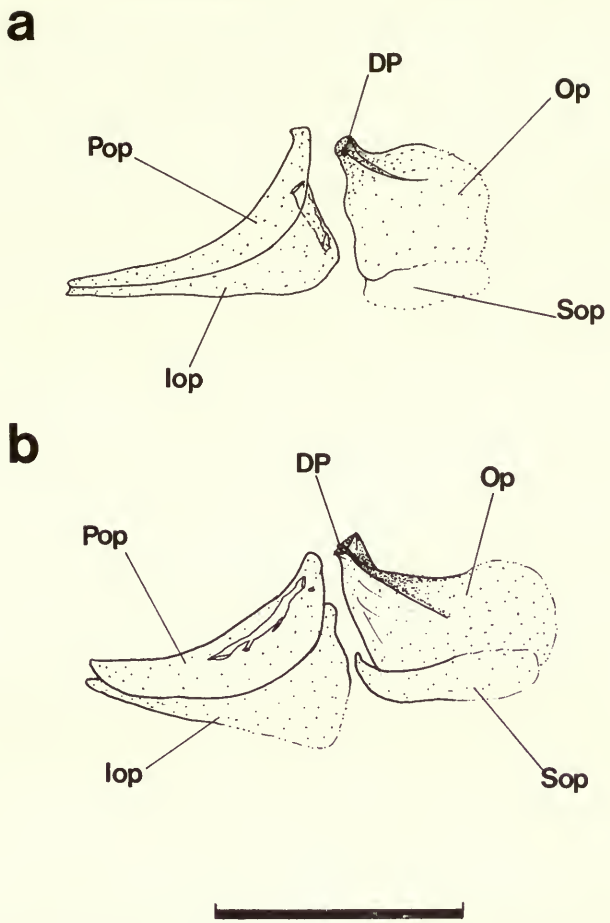


Fig. 18 Opercular series of (a) *Chaudhuria caudata* and (b) *Pillaia indica.*

Hyoid and branchial arches

The *basihyal* is spatulate with a low ventral ridge, and has its posterior end connected to the anterior end of basibranchial 1 (Fig. 20ai).

The *dorsal* and *ventral hypohyal* bones are connected to the posterolateral face of the basihyal across its border with basibranchial 1 (Fig. 20ai). These elements are connected to each other and the proximal end of the anterior ceratohyal by a narrow cartilaginous interface. The dorsal hypohyal is pierced by a large central foramen for the passage of the hyoidean artery. Dorsal to this foramen its medial face is faceted and articulates with the anterolateral face of basibranchial 1. The compressed anterior region of the ventral hypohyal has a medial facet that contacts its partner in the midline ventral to the posterior end of the basihyal.

The *anterior ceratohyal* is hatchet-shaped, in lateral view, and supports the base of the 3rd and 4th branchiostegal rays distally on its wide anterior face. (Fig. 19a). The narrow proximal end supports the 1st and 2nd branchiostegal rays. A single process extends from its lateral end and is housed in a recess on the posterior face of the posterior ceratohyal. Apart from this projection the ceratohyals are connected only by a straight suture incorporating a wide cartilaginous interface.

The *posterior ceratohyal* has a wide ventral lip that supports, on its posterior face, the base of the 1st and 2nd branchiostegal rays. The distal end of this bone is connected by a tough ligament to the interhyal.

The *interhyal* is a short rod-shaped bone that is joined to the fibrous connective tissue between the symplectic and hyomandibula, medial to the preoperculum (Fig. 19a).

The *urohyal* is forked anteriorly with each tip ligamentously connected to the ventral hypohyal. Posteriorly, it increases in depth and is relatively short, terminating at a point ventral to basibranchial 4 without developing into prong-like processes.

Basibranchial 1 is a short, cylindrical element without a ventral keel. Anterolaterally it articulates with the medial face of the dorsal hypohyal, and posteriorly with basibranchial 2 (Fig. 20ai).

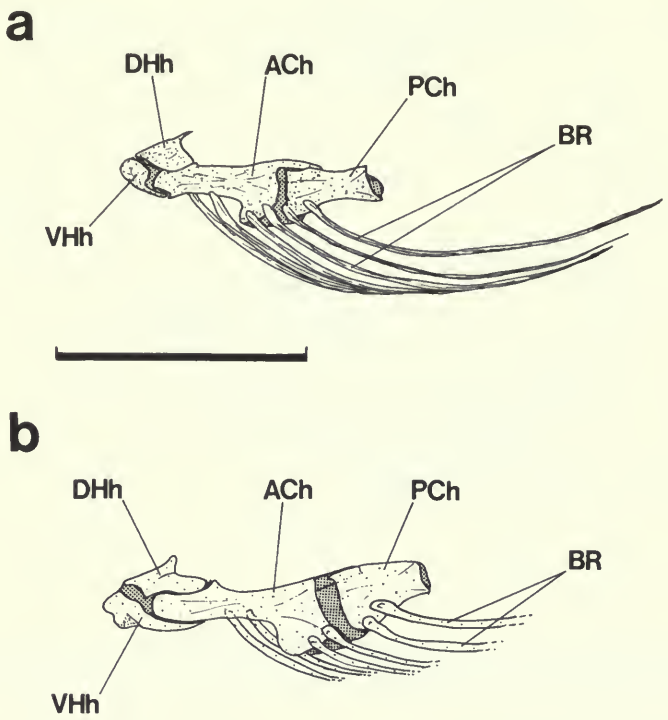


Fig. 19 Hyoid arch, in (a) *Chaudhuria caudata* and (b) *Pillaia indica*; lateral view, left side.

Basibranchial 2 is rod-like and the medial face of hypobranchial 1 connects to its anterolateral face. There are no ventral processes and posteriorly it is joined to basibranchial 3.

Basibranchial 3 is long and its tapered posterior end terminates in a cartilaginous tip (Fig. 20ai). The medial end of hypobranchial 2 is connected to the anterolateral face of basibranchial 3.

Basibranchial 4 is a small cartilaginous element (Fig. 20ai). Its anterolateral face is connected to the medial end of hypobranchial 3, and its posterolateral face to the medial end of ceratobranchial 4.

Hypobranchials 1 and 2 are relatively short rod-like bones distally connected to the anterior (medial) end of their corresponding ceratobranchials (Fig. 20ai).

Hypobranchial 3 is shorter and broader than its anterior counterparts; its anterior process is relatively short and does not extend below hypobranchial 2 (Fig. 20ai). A round toothplate with small caniniform teeth is fused to the dorsal surface.

Ceratobranchials 1–5 are long, rod-like bones, all, apart from the 5th, essentially similar. The distal ends of ceratobranchials 1–4 are joined by connective tissue to the distal ends of the corresponding epibranchial bones. The ventral surface of each ceratobranchial is grooved and accommodates the bases of the gill filaments.

Ceratobranchial 5 carries a fused toothplate which has a slight medial expansion and bears relatively large caniniform teeth (Fig. 20ai). Posterior to its toothplate, ceratobranchial 5 curves dorsolaterally to form a process for muscle attachment. All dorsal gill arch elements lie posterior to the neurocranium, as do some of the ventral elements.

Epibranchials 1 & 2 are but slightly curved, narrow bones (Fig. 20aii). The medial end of epibranchial 1 is connected to the anterior end of the small rod-like pharyngobranchial 1, and epibranchial 2 connects with its posterior end.

Epibranchials 3 and 4 both have an ascending uncinate process (Fig. 20aii). The dorsal tips of these processes are connected by a short strand of collagenous tissue. The medial end of epibranchial 3 is connected to the posterolateral margin of pharyngobranchial 3. The medial end of epibranchial 4 is broad and is joined to the wide posterior end of pharyngobranchial 3.

Pharyngobranchial 2 and 3 are the only pharyngobranchial (infrapharyngobranchial) bones present. Pharyngobranchial 2 is a small, untoothed element that lies between the proximal ends of epibranchials 1 and 2 (Fig. 20aii). Pharyngobranchial 3 is a much larger bone and bears a large toothplate fused to its ventral surface. The proximal end of pharyngobranchial 3 is connected to the distal end of pharyngobranchial 2 and together these are joined to the tip of epibranchial 2. The distal end of pharyngobranchial 3 is broad and connected to the wide proximal face of epibranchial 4. The proximal end of epibranchial 3 is not connected to the distal end of pharyngobranchial 3 but is connected to its posterolateral margin. A large toothplate lies below the proximal end of epibranchial 4 and is the pharyngobranchial 4 toothplate, although there is no sign of its corresponding bone. This toothplate and that on pharyngobranchial 3 have relatively large caniniform teeth with posteriorly directed tips.

Pectoral girdle

The pectoral girdle lies posterior to the neurocranium, adjacent to the 3rd and 4th abdominal vertebrae. It lacks a posttemporal connection to the neurocranium and there are no posttemporal canal tubules surrounding the postcranial sensory canal anterior to the supracleithrum.

The *supracleithrum* is a small sinusoidal element (Fig. 21ai). The postcranial laterosensory canal passes through its dorsolateral face; ventrally it overlaps the dorsolateral face of the cleithrum to which it is loosely connected.

The *cleithrum* is bowed and has a narrow lateral face. Dorsally it contacts the supracleithrum, ventrally it meets its partner in a median symphysis (Fig. 21ai).

Apart from these two bones the pectoral girdle consists only of two indistinct cartilaginous elements that lie posterior to the cleithrum, are partly fused anteriorly and appear to support the fin rays. These rays are indistinct in the specimens examined although Annandale & Hora (1923) described 7 segmented pectoral fin rays in *Chaudhuria.*

Vertebral column

The total vertebral count is 72, *viz.*, 25 abdominal, 46 caudal and the fused ural and first preural centra.

The unusual form of the vertebrae in *Chaudhuria* has been described by Annandale (1918). The first 6 *abdominal vertebrae* have antero-posteriorly expanded neural spines (Fig. 21aii). Those on the subsequent centra are subdivided into an anterior and posterior peak, giving the neural arch on these vertebrae the appearance of having two spines. A short neural projection anterior to the spine occurs on all abdominal vertebrae apart from the 1st–6th. The anterior spine is directed dorsally and less backwards than the posterodorsally directed posterior spine. It decreases in height posteriorly and is absent from the caudal vertebrae apart from a slight projection on the first three or four of these elements.

The neural arches of the anterior abdominal vertebrae have a densely perforated lateral surface. The anterior end of the 1st abdominal centrum is rounded to form a hemispherical condyle that articulates with the tripartite occipital socket in a 'ball and socket' joint.

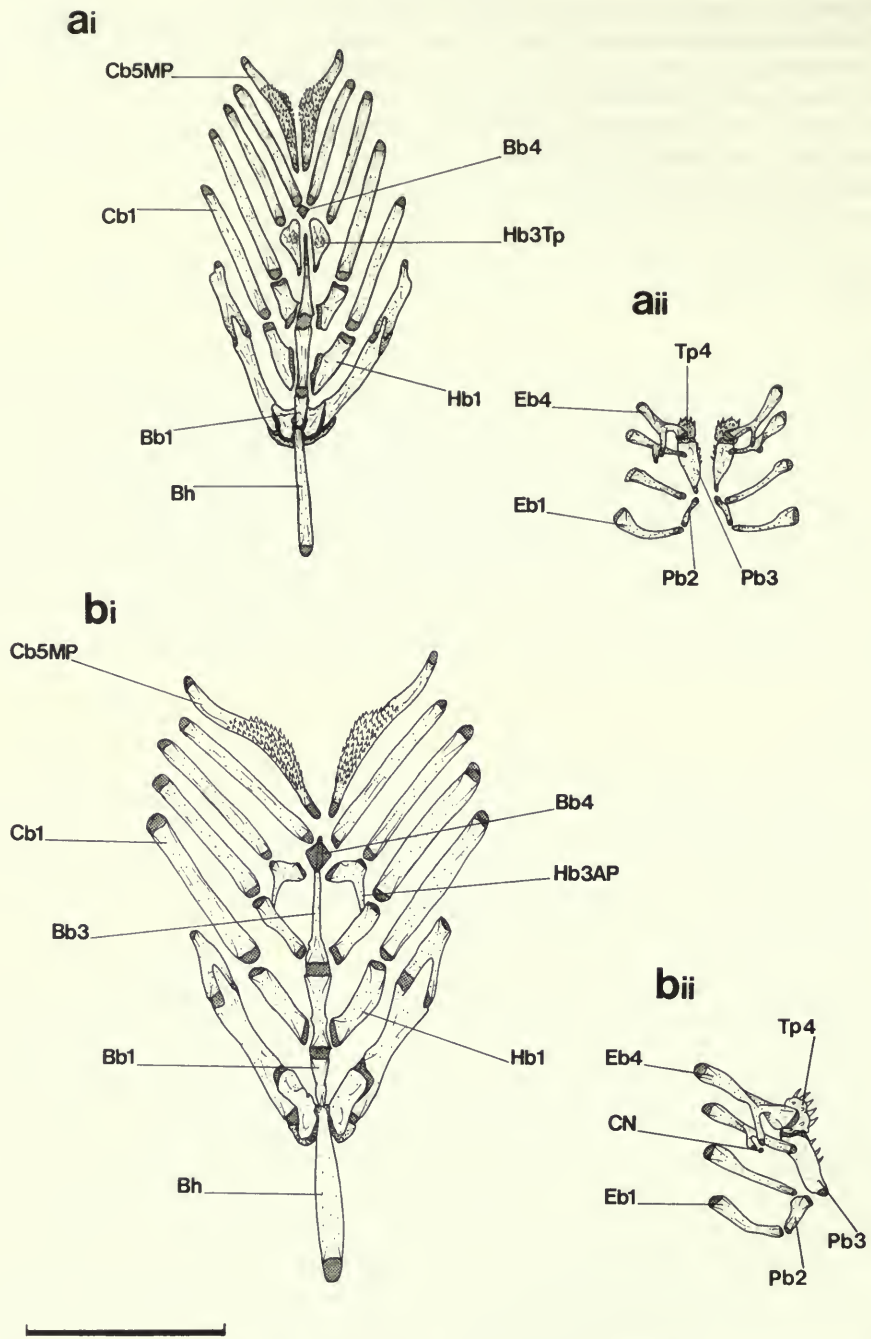


Fig. 20 Hyobranchial arches in (a) *Chaudhuria caudata* and (b) *Pillaia indica*; dorsal view of lower bones (ai & bi), and upper bones (aii & bii).

Pre- and postzygapophyses are well developed on all but the 1st abdominal vertebra. Laterally directed parapophyses occur on this and all subsequent abdominal vertebrae; apart from those on the 1st–3rd vertebrae, their tips curve ventrally.

Epicentral ribs occur on the 1st abdominal vertebra only, and *epipleural ribs* are absent.

Pleural ribs are present on the 4th and all succeeding abdominal vertebrae. They are supported in a groove along the posterior face of the parapophyses. A small bone lies posterior to the tip of the parapophysis on the 3rd abdominal vertebra and may represent a pleural rib. The *caudal vertebrae* have short, narrow neural and haemal spines. The abdominal and caudal centra are characterised by their asymmetry which is gradually lost posteriorly.

Dorsal and anal fins

Dorsal and anal spinous rays and their supporting pterygiophores are absent.

Forty *dorsal* and *anal branched fin rays* extend from a point above and below the abdominal/caudal vertebral junction to the 7th or 8th preural vertebra. Each fin is supported by a pterygiophore system composed of 3 elements; a large well ossified *proximal pterygiophore* fused to a cartilaginous *medial pterygiophore*, and a small independent *distal pterygiophore*. The lack of fin rays (and their supporting pterygiophores) on the posterior 6 or 7 caudal vertebrae is a diagnostic feature of *Chaudhuria* originally described by Whitehouse (1918).

Caudal fin

The caudal fin is distinct from the dorsal and anal fins and is composed of 8 segmented fin rays.

Two *hypural* bones (possibly composed of hypurals 1+2, and 3+4+5+6) fan out from the fused ural and first preural centra (Fig. 23a). These elements are autogenous and each supports 4 fin rays along its cartilaginous posterior margin.

A small *parhypural* is fused along the ventral edge of the hypaxial hypural.

The *uroneural* is small and appears to be fused along the dorsal edge of the fused ural and first preural centra. There is a single *epural* bone. The 2nd preural vertebra has a fused neural and haemal arch with short spines which do not support fin rays.

Squamation

The body is entirely *scaleless*.

Osteology of *Pillaia indica*

This description is based on two specimens (both on loan from the ZSI; see Table 3). The larger specimen (68mm. standard length) is poorly preserved and stained (alizarin only). The second individual is smaller (only 44.5 mm. long) but has responded well to both stains (alizarin & alcian blue), and its internal anatomy is clearly visible.

Neurocranium

Ethmovomerine region

The *supraethmoid* is similar to that described in *Chaudhuria* (p. 32 Fig. 15ai) apart from a notch in the anterodorsal edge which houses a small rostral cartilage (Fig. 15bi).

The *vomer* is curved posteroventrally and extends to a point adjacent to the middle of the ascending lateral walls on the parasphenoid (Fig. 15bi). The long anterior arm of the ectopterygoid lies along the posterolateral face of the shaft (discussed below).

Each *lateral ethmoid* consists of a thin medial wall from which a stout, curved strut arches laterally giving it a somewhat tubular shape (Fig. 15bi). The medial wall contacts its partner in the midline, dorsal to the cartilaginous region of the supraethmoid, and the lateral face articulates syndesmotically with a medial facet on an ascending process on the 1st infraorbital bone. Below this connection the lateral ethmoid is drawn out into a tapered anteroventral process that lies along the dorsolateral margin of the vomerine shaft. The anterior end of the suspensorium lies adjacent to this process, but there is no direct contact.

The *nasal* is a weakly ossified, flattened bone (Fig. 15bi) that slopes ventrolaterally and overlies the olfactory cavity in a manner corresponding closely to that in *Chaudhuria* (Fig. 15ai). A number of small, irregular pores pierce the posterodorsal surface.

Orbital region

The lateral face of the orbital region is open and there is no sign of *pterosphenoid* or *basisphenoid* bones. The *parasphenoid* has a short anterior process, possibly associated with the small orbital cavity, which is bent dorsorostrally and terminates at a point below the lateral ethmoid (Fig. 15bii). A wide lateral wall ascends from the parasphenoid and, apart from contacting the posteroventral edge of the prootic, is unattached to any other bone. Posteriorly, the lateral wall narrows to a reduced shaft and from this region the parasphenoid is divided into a pair of long, needle-like processes which extend across the posteroventral edge of the basioccipital.

The *1st infraorbital* bone is the only element of the infraorbital series. Ventrally it is connected to the dorsal surface of the upper jaw element.

Otic region

The *prootic* lies between the posterolateral wall of the parasphenoid and the sphenotic. The trigeminofacialis chamber is similar to that described in *Chaudhuria* (p. 33), but anterior to it the prootic in *Pillaia* has a short, blunt projection that is unattached to any other bone. The posterior region of the prootic borders the pterotic, exoccipital and basioccipital bones and houses the anterior third of the relatively large sacculus.

The *sphenotic* has a long tapered anterior projection that passes along the dorsolateral edge of the frontal (Fig. 15bi). The tip of this process extends to a point adjacent to the anterior end of the parasphenoid lateral wall. This region of the sphenotic is unconnected to any other bone. The ventral edge contacts the prootic and forms the anterodorsal rim of the single large foramen in the pars jugularis. A low postorbital process dorsal to the lateral commissure in the trigeminofacialis chamber, is just discernible. The posterior position of this process (relative to the orbit) illustrates that the main region of neurocranial elongation in *Pillaia* is precommissural. Posterior to the process the neurocranium is of more typical perciform proportions.

The *pterotic* has an inflated lateral face and the dorsal edge is overlapped by the dorsolateral margin of the parietal. The ventral surface is grooved and accommodates the posterior hyomandibular condyle (Fig. 15bi). Below this groove the pterotic contacts the prootic and exoccipital. There is no posttemporal fossa although the ventral margin forms part of the roof of a recess in the lateral wall of the basicranium.

The *epioccipital* is small and forms, in conjunction with the exoccipital and supraoccipital, the posterodorsal wall of the basicranium (Fig. 15bi & iii).

The dorsomedial process on the *exoccipital* is prevented from contacting its partner in the midline by the posterior end of the supraoccipital. The dorsal surface is pierced by numerous small perforations. Three major foramina pierce the posteroventral face. Below their midline connection each exoccipital has a somewhat concave deltoid facet which contributes to the tripartite occipital facet (a concave socket) that articulates with the rounded anterior half of the first abdominal centrum (Fig. 21bii).

The large *basioccipital* relative, that is, to its size in other mastacembeloids, contacts the prootic anteriorly and the exoccipital dorsally. The tips of the parasphenoid ventral processes extend beyond its posteroventral edge. A facet on the posterior face contributes to the occipital facet.

The *supraoccipital,* which is also relatively large, lacks any form of sculpturing, is transversely convex and bounded on either side by the parietals and by a posterior extension of the frontals. All these surrounding bones overlap its margin. Posteriorly, contact is made with the exoccipitals, and the supraoccipital contributes to the rim of the foramen magnum (Fig. 15biii).

The *extrascapulae* (both lateral and medial) and the *posttemporal* are absent.

The flattened *frontal* lacks a descending lamina, crests, or any form of sculpturing. Anteriorly it has a relatively short, narrow region (dorsal to the small orbit), which overlies the lateral ethmoid; the longer posterior part is curved ventrolaterally.

The *parietal* is small compared with this bone in *Chaudhuria* and other mastacembeloids. It has a narrow dorsal surface and a short posterolateral flange which lies along the dorsal junction between the epioccipital and exoccipital. A distinct notch in the posteromedial edge of the parietal forms, with the supraoccipital, a small opening in the posterior surface of the neurocranium (Fig. 15biii).

Only short branches of the *cephalic sensory canal system* occur in the preoperculum, dentary, frontal, 1st infraorbital and nasal bones, and are presumably inter-connected by dermal branches.

Jaws

The single *upper jaw* element has been described by Yazdani (1976*a* & *b*; 1978). This element appears from its shape to incorporate the premaxilla with the maxilla, and may well have formed during ontogeny by the fusion of these bones (see discussion on p. 37, Fig. 16b). A short flange on the anteromedial face of the upper jaw bone articulates with the faceted anterior end of the vomer. The ventral surface is alveolate and bears an outer row of long caniniform teeth, and 1 to 2 inner rows of small teeth, decreasing in size posteriorly.

Each *dentary* is joined to its partner in a symphysis lying in the vertical below the upper jaw symphysis. A short symphysial process descends from the anteroventral edge of the dentary. The coronoid region is developed into a relatively tall, shallow process and is covered laterally by the posteroventral limb of the upper jaw. The alveolar surface along the dorsal edge (anterior to the coronoid process), bears an outer row of large caniniform teeth, relative to the size of the jaw, and 2 to 3 inner rows of smaller teeth. The posteroventral arm extends as a long pointed process along the ventral edge of the anguloarticular. A short sensory canal lies within the dentary which is pierced by three pores.

The *anguloarticular* is a long tapered bone (Fig. 16b), and has a straight dorsal edge apart from a low projection anterior to the deep facet on the posterodorsal corner. Meckel's cartilage is long, rod-like, and passes along the medial face into the dentary.

The *retroarticular* is small and roughly L-shaped with a very short lower arm (Fig. 16b). Except for its dorsal connection the retroarticular is free from the posteromedial face of the anguloarticular. The interopercular ligament is connected to the free posteroventral edge.

The small *coronomeckelian* is similar to that in *Chaudhuria* (Fig. 16).

Hyopalatine arch

The *hyomandibular* shaft is short; a wide flange situated on its anterolateral face is connected anteriorly to the metapterygoid, and ventrally to the dorsal edge of the symplectic in an arrangement that corresponds closely to that seen in *Chaudhuria* (Fig. 17a & b).

The long *symplectic* has a narrow lateral face and no dorsal lamina. Its anterior end lies below the posteromedial face of the quadrate.

The *metapterygoid* has a small anterodorsal projection which, together with the bone's anterior edge, is separated from the quadrate by a cartilaginous interface.

The *quadrate* has a straight anterior edge which ventrally forms a stout condyle for articulation with the anguloarticular facet.

The *endopterygoid* is absent.

The long *ectopterygoid* has a narrow lateral face and only its posterolateral margin lies medial to the anterodorsal corner of the quadrate (Fig. 17b). The anterior end is curved anteromedially and its medial face is loosely joined by connective tissue to the vomerine shaft. This connection is the anterior point of articulation between the suspensorium and neurocranium.

The *palatine* is absent. It may be incorporated into the anterior arm of the ectopterygoid,

possibly by fusion, during ontogeny. The lack of direct articulation between the ectopterygoid and lateral ethmoid, and the absence of a palatine, were not recognised by Yazdani (1976*b*:168) who described: narrow palatines '... movably united to parasphenoid and vomer' and the '... pterygoid (ectopterygoid) movably united to lateral ethmoid outside the palatine'.

Opercular series

The *preoperculum* lacks distinct vertical and horizontal arms (Fig. 18b), and is thus crescentic in shape. The lateral face of the preoperculum is wide and accommodates a short, indistinct sensory canal (as discussed above).

The *interoperculum, suboperculum* and *operculum* are generally poorly ossified (Fig. 17b) and are arranged as in *Chaudhuria* (p. 38).

Hyoid and branchial arches

The *basihyal* is straight with a low ventral ridge. Posteriorly it overlies the anterior tip of basibranchial I (Fig. 20bi).

The paired *dorsal* and *ventral hypohyal* bones, the *anterior* and *posterior ceratohyals* and the *interhyal*, closely correspond with the same elements in *Chaudhuria* (see above, p. 39 and Fig. 19 a & b).

The *urohyal* is forked anteriorly, posterior to this point a low ridge ascends from the dorsal surface ventral to basibranchial 2. The posterodorsal corner of the ridge is connected by a diverging ligament to the anterior tips of each hypobranchial 3.

Basibranchial 1 lacks a ventral keel.

Basibranchial 2 is narrow-waisted and lacks ventral processes.

Basibranchial 3 is particularly long and tapered posteriorly; its cartilaginous tip lies ventral to basibranchial 4 (Fig. 20bi). This rod-like region is capable of sliding below basibranchial 4 when the branchial arches contract.

Basibranchial 4 is a rhomboidal cartilaginous element (Fig. 20bi). Its anterolateral wall is connected to the medial edge of hypobranchial 3, and its posterolateral wall to the medial end of ceratobranchial 4.

Hypobranchial 1 and 2 are cylindrical apart from a slight prominence along the anterior margin.

Hypobranchial 3 is a small bone with a distinct, long and tapered anterior process which terminates below hypobranchial 2 (Fig. 20bi). The tip of this process is connected ligamentously to the posterior edge of the low ridge on the urohyal. The hypobranchial 3 toothplate is absent.

Ceratobranchials 1–5 are rod-like elements and with the exception of the 5th are essentially alike. The dorsal surface of ceratobranchial 5 supports a narrow, fused toothplate bearing relatively large caniniform teeth. Posterior to its toothplate, ceratobranchial 5 curves dorsally into a relatively long process for muscle attachment (Fig. 20bi).

All the dorsal gill arch elements lie posterior to the neurocranium and are essentially similar to those found in *Chaudhuria* (Fig. 20aii).

Pectoral girdle

The pectoral girdle lacks a bony connection to the neurocranium and lies posterior to the skull, adjacent to the 3rd and 4th abdominal vertebrae. Posttemporal sensory canal tubules are absent.

The *supracleithrum* is small (Fig. 21bi) and accommodates a section of the postcranial sensory canal in its dorsolateral face.

The *cleithrum* is a stout bone relative to the size of the other pectoral elements, is bowed and meets its partner in a ventral symphysis. The dorsal end is pointed and its posterior edge deeply grooved (Fig. 21bi).

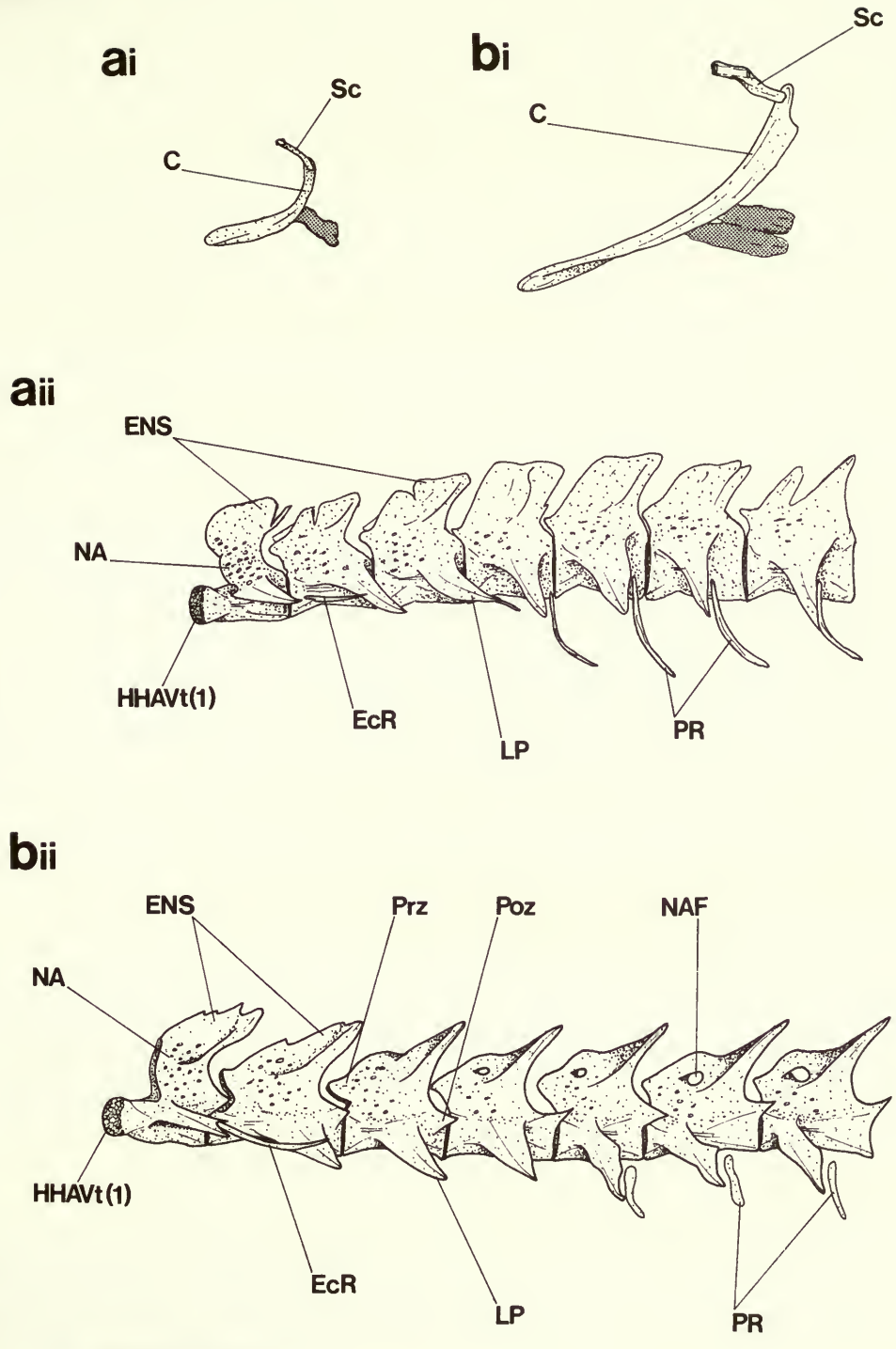


Fig. 21 Postcranial skeleton in (a) *Chaudhuria caudata* and (b) *Pillaia indica*; lateral view (left side) of pectoral girdle (ai & bi) and anterior abdominal vertebrae (aii & bii).

The remaining pectoral elements are small, ill-defined and cartilaginous. The fin rays do not appear to have differentiated in the specimens I examined, but Yazdani (1978) records 6 rays in the pectoral fin.

Vertebral column

The total vertebral count is 66, *viz.*, 28 abdominal, 37 caudal and the fused ural and first preural centra.

The first two *abdominal vertebrae* have compressed neural spines; that on the 1st has a serrated dorsal peak. The neural arches of these vertebrae have a perforated dorsolateral surface; anteroventral to the neural spine, a large foramen pierces the lateral face of the neural arch on all but the first 3 abdominal vertebrae. The anterior end of the 1st abdominal centrum is rounded to form a hemispherical condyle that articulates with the tripartite occipital socket in a 'ball and socket' joint.

Pre- and postzygapophyses are well developed on all but the 1st abdominal vertebra which also lacks a well developed parapophysis. Laterally directed parapophyses occur on the 2nd, 3rd and 4th vertebrae but on the 5th they are curved ventrally, becoming increasingly so on all succeeding abdominal vertebrae.

Along the abdominal vertebrae there is a total of 1 pair of epicentral and 24 pairs of pleural ribs.

The pair of *epicentral ribs* occurs on the 1st vertebra (Fig. 21bii). This vertebra lacks lateral parapophyses and the anterior end of each rib is lodged in a recess within the posterolateral margin of the centrum, ventral to the postzygapophysis. The rib extends posteriorly to a point beyond the 2nd vertebra and its tip is connected by a short ligament to the dorsomedial face of the cleithrum.

Pleural ribs are present on the 5th and all succeeding abdominal vertebrae. They are supported in a groove along the posterior face of the lateral parapophyses (Fig. 21bii).

The *caudal vertebrae* have short, narrow neural and haemal spines and on some of the posterior vertebrae the spines have forked tips. A deep notch in the dorsolateral margin of the neural arches (Fig. 22, anterolateral to the neural spines) appears to have developed by the expansion of a foramen seen in the neural arches from the more posterior abdominal vertebrae.

The asymmetry of the abdominal and caudal centra is gradually lost posteriorly.

Dorsal and anal fins

Dorsal and *anal spinous rays* and their supporting pterygiophores are absent.

The *dorsal* and *anal branched fin rays* are composed of 35 and 36 segmented elements respectively. They extend, from a point above and below the abdominal/caudal vertebral junction, to the dorsal and ventral edge of the caudal fin, with which they are confluent. Each ray is supported by a pterygiophore system composed of 3 elements (Fig. 22).

The *proximal pterygiophore* is a long, well-ossified element. Its distal end is fused to a medial pterygiophore. The rod-like *medial pterygiophore* is cartilaginous and lies anterior to the small, independent and ossified *distal pterygiophore.*

Caudal fin

The caudal fin is composed of 10 segmented fin rays which, although confluent with the posterior rays of the dorsal and anal fins, extend posteriorly well beyond their tips.

Two *hypural* bones fan out from the fused ural and first preural centrum (Fig. 23b), these probably represent the fused 1st+2nd & 3rd+4th+5th+6th hypurals found in more primitive teleosts. The elements each support 5 fin rays along their cartilaginous posterior margin. A small *parhypural* is sutured along the ventral edge of the hypaxial hypural. The epaxial hypural, the ural and first preural centra are fused into a single element (Fig. 23b).

The *uroneural* is fused along the dorsal edge of the fused ural and first preural centra. There is only a single short *epural* which has a barbed, leading edge.

The 2nd preural vertebra has fused neural and haemal arches. The corresponding spines are short and do not support fin rays. The tip of the haemal spine is forked as it is on the 3rd, 4th and 6th preural vertebrae. The neural spines are forked on the 5th and 6th preural vertebrae.

Squamation

The body is entirely *scaleless.*

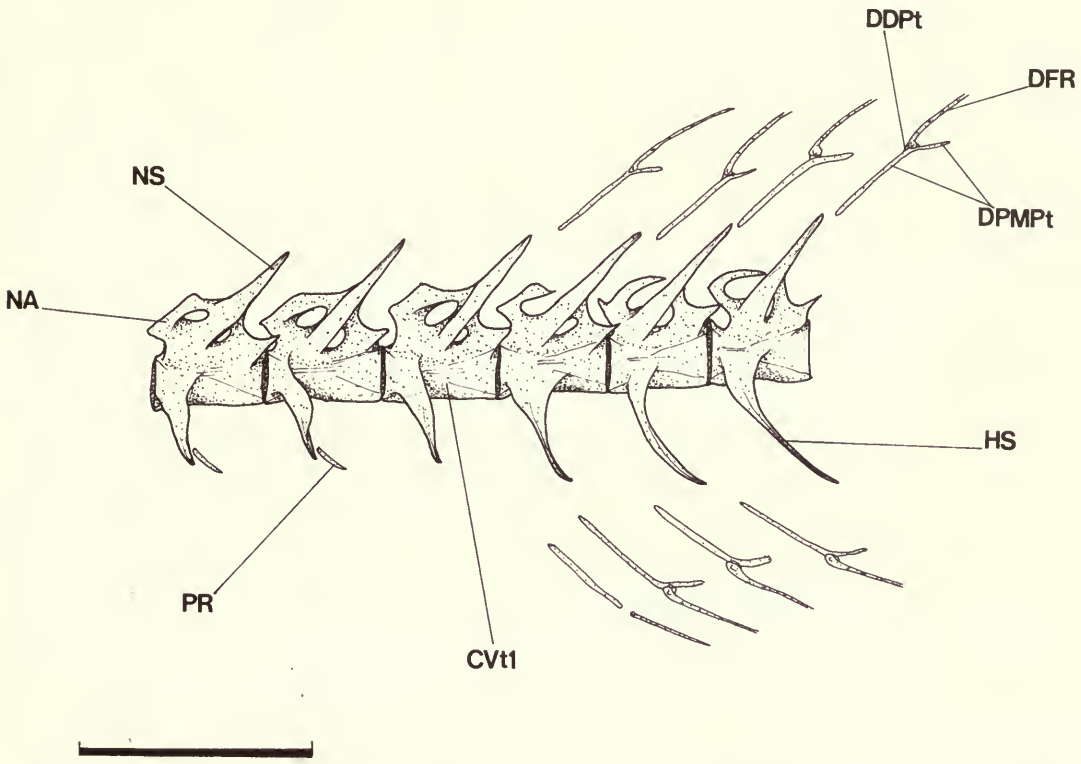


Fig. 22 *Pillaia indica,* abdominal/caudal vertebral junction and associated dorsal and anal fin rays: lateral aspect, left side.

Comparative osteology of the Mastacembeloidei

The osteological descriptions of *Mastacembelus mastacembelus, Chaudhuria caudata* and *Pillaia indica* are used here as the basis for a comparative osteological study of all available mastacembeloid species (see list of study material, Table 3). Each major osteological functional unit within a species is compared with its condition in *M. mastacembelus* in order to identify interspecific differences and similarities. Whether these character states are apomorphic or plesiomorphic for the group as a whole, or for any sublineage, and thus their value as indicators of phylogenetic relationships is considered in the sequal to this study (Travers, 1984).

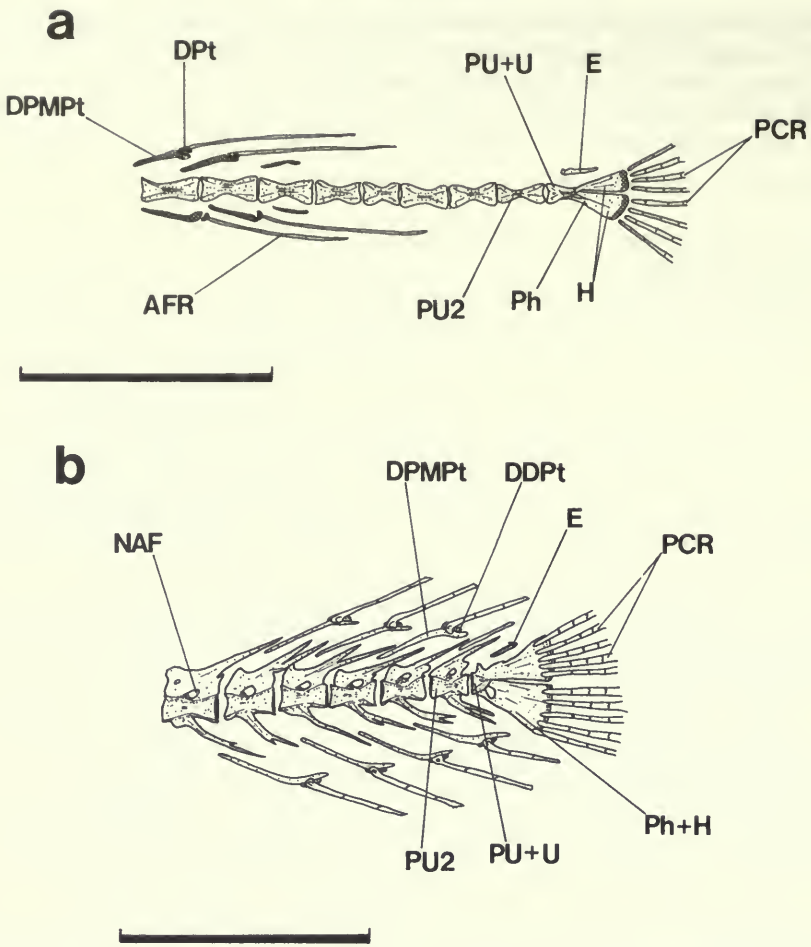


Fig. 23 Posterior caudal vertebrae, associated fin rays and caudal fin skeleton in (a) *Chaudhuria caudata* and (b) *Pillaia indica*; lateral view, left side.

Neurocranium

Ethmovomerine region

The condition of the ethmovomerine region in *Mastacembelus mastacembelus* (Fig. 1a) is typical of that found in most mastacembeloids.

The posterolateral face of the *supraethmoid* septum is pierced by a fenestra in *M. longicauda* and *M. reticulatus* from West Africa (Fig. 33). A similar fenestra is also found in *M. sclateri* (Fig. 33d), although in this species it notches the posterodorsal edge of the supraethmoid. The fenestra is generally covered by a membrane and serves as the site of origin for the oblique eye muscles.

Vomerine teeth were recorded by Regan (1912) although they are absent in all specimens I examined; Regan may well have misidentified the small toothplate that sometimes occurs on the anteroventral surface of the palatine.

The near tubular *lateral ethmoid* is characteristic of both Asian, including the Middle Eastern, and African species. The centre of the lateral ethmoid in *Mastacembelus marchii* is subdivided by a median partition into two distinct tube-like canals.

The ventral edge of the posterior opening in the lateral ethmoid in *M. maculatus* (Fig. 26a) is curved posteroventrally as it is in the West African species *M. goro, M. greshoffi,*

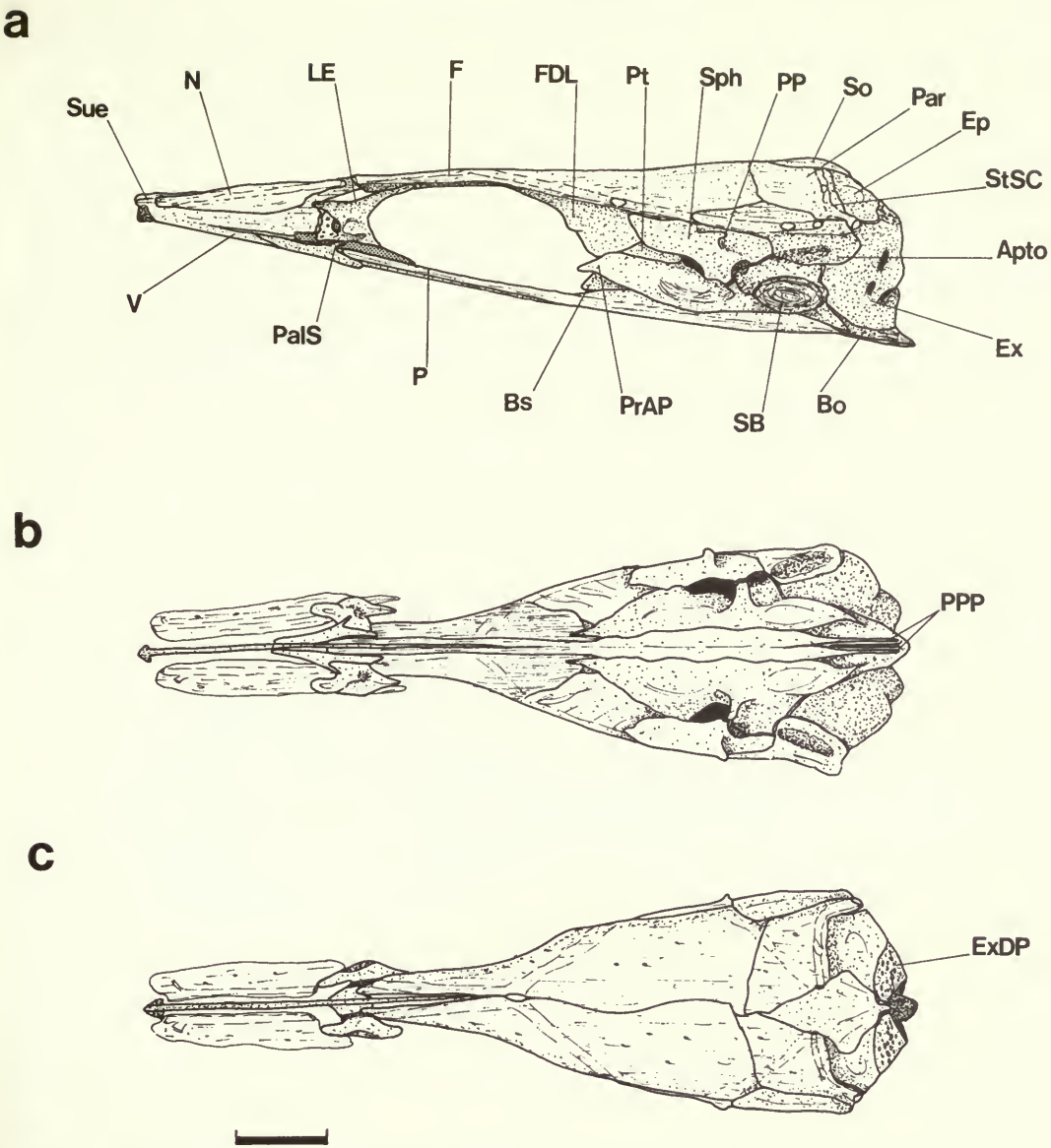


Fig. 24 *Mastacembelus sinensis,* neurocranium in (a) lateral view, left side, (b) ventral view and (c) dorsal view.

M. longicauda, M. loennbergii and *M. niger.* This ventral projection lies along the dorsal edge of the cartilaginous posterior end of the supraethmoid. The dorsal surface is grooved longitudinally to accommodate the anterior end of the large *nervus olfactorius* (p. 13) and the tip may contact the pterosphenoid (e.g. *M. maculatus* Fig. 26a).

Orbital region

In a number of taxa the morphology of the orbital region departs considerably from that of *M. mastacembelus.*

The *pterosphenoid,* which generally forms a part of the anterolateral wall to the cranial cavity, is absent in *Chaudhuria* (Fig. 15ai) and *Pillaia* (Fig. 15bi). It is small in

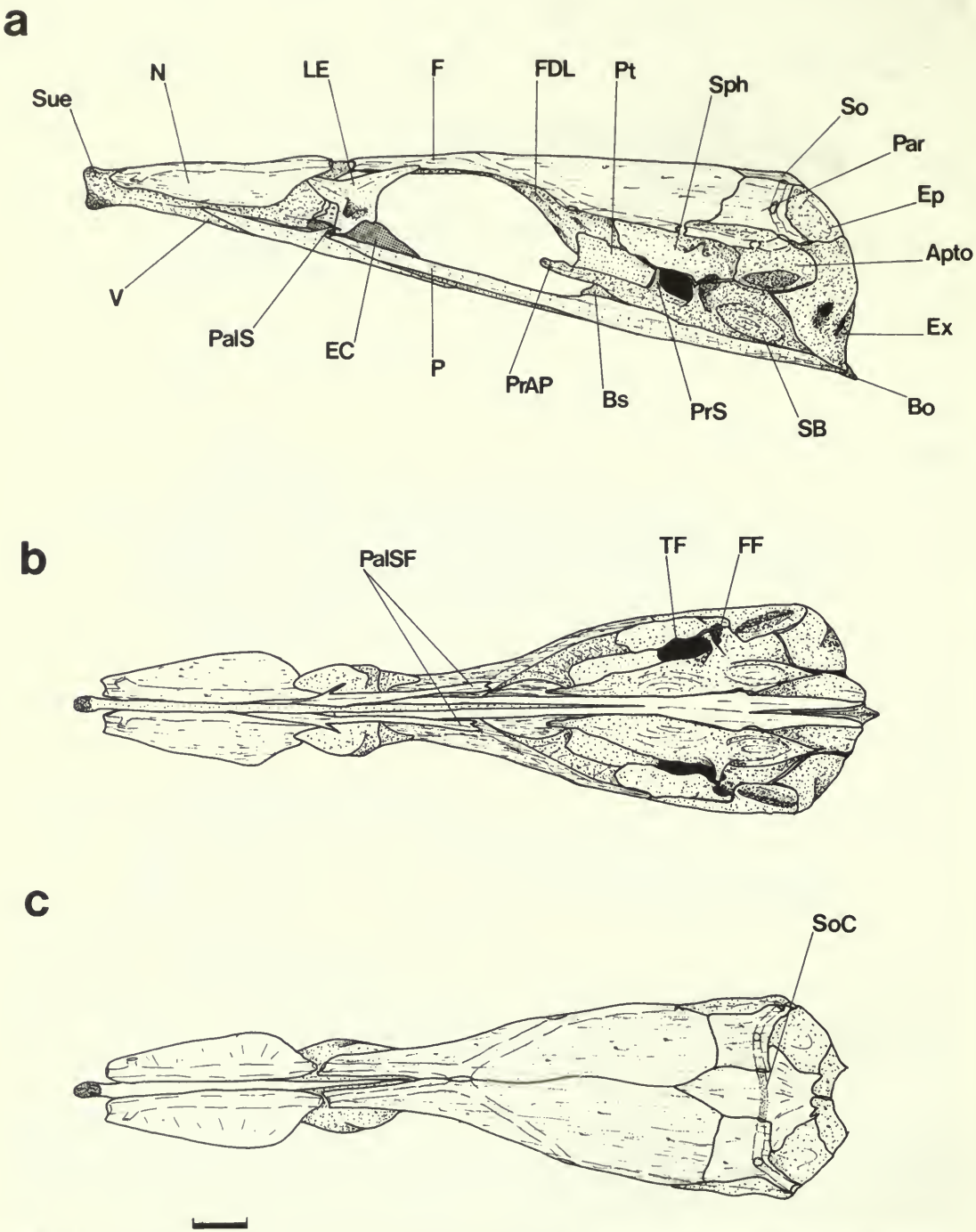


Fig. 25 *Mastacembelus erythrotaenia,* neurocranium in (a) lateral view, left side, (b) ventral view and (c) dorsal view.

Mastacembelus aviceps (Fig. 40 a & b), a microphthalmic species from the lower Zairean rapids (Roberts & Stewart, 1976), and is discernible only as a splint-like bone sutured to the ventrolateral edge of the frontal.

The posterior and anterior connections of the pterosphenoid may also differ from those in *M. mastacembelus* (p. 14). Posteriorly, it does not contribute to the rim of the trigeminal foramen in a number of species both among the Asian (e.g. *M. erythrotaenia,* Fig. 25a) and African (e.g. *M. frenatus,* Fig. 31a) taxa; in these the anterior rim of the trigeminal foramen is formed by the prootic and sphenotic.

The anterior edge of the pterosphenoid is partly restricted from bordering the postorbital edge of the neurocranium in four African species; *M. micropectus* (from Lake Tanganyika), *M. stappersii* (from Zaire), *M. goro* and *M. batesii* (from Cameroon). In these species the descending frontal lamina is particularly large and curves ventromedially, contacting its partner in the midline. The optic foramen in these species is predominantly enclosed by the frontals.

A *basisphenoid* is present in almost all mastacembeloids, (*pace* Regan, 1912; Bhargava, 1963*a*; and Maheshwari, 1965*a*), although it may be obscured in lateral view by the prootic, pterosphenoid and parasphenoid (Taverne, 1980). A large basisphenoid (relative to that in *M. mastacembelus*) occurs in *Macrognathus* species (*M. siamensis, M. aral,* and *M. aculeatus*), and to a lesser extent in *Mastacembelus zebrinus* among the Asian species and *M. shiranus, M. congicus, M. liberiensis, M. longicauda* and *M. loennbergii* among the African species. In these fishes the dorsal tip of the basisphenoid bridges the ventromedial edge of each pterosphenoid, which is incompletely sutured in the midline. A relatively large basisphenoid is associated with a greater distance between the pterosphenoid and parasphenoid bones, and consequently with a less depressed orbital region than that in *M. mastacembelus* (Fig. 1a) or in other species with a small basisphenoid.

The posterior edge of the large basisphenoid in *M. shiranus, M. congicus, M. liberiensis, M. longicauda* and *M. loennbergii* contributes, with the pterosphenoid, parasphenoid and anterior process of the prootic, to the formation of a large lateral foramen in the anteroventral wall of the neurocranium (Figs. 32a & 33a). This forms an unusually wide opening to the posterior myodome which in other species is generally a small foramen obscured, in lateral view, by the prootic. In *Macrognathus aculeatus* (Fig. 30a) and *Mastacembelus zebrinus* (Fig. 27a) the basisphenoid is particularly large and consequently there is a characteristically wide opening to the posterior myodome.

The basisphenoid is absent only in *Chaudhuria* and *Pillaia* among the Asian, and *Mastacembelus brichardi, M. crassus* and *M. aviceps* among the African taxa (Figs. 39a & 40a: possibly *M. latens* should be included here as well).

The general arrangement of the *parasphenoid* described in *Mastacembelus mastacembelus* (p. 14) is found in the majority of mastacembeloid taxa. However, there is interspecific variation in the posterior region of this bone. In *Chaudhuria* and *Pillaia,* and to a lesser extent in *Mastacembelus sinensis* (Fig. 24b), the posterior parasphenoid processes are particularly long and narrow. They are distinguished in *Chaudhuria* and *Pillaia* at a point below the medial connection between the prootics (slightly posterior to this point in *M. sinensis*), and extend posteriorly as long, pointed processes to the posterior edge of the basioccipital.

The posterior region of the parasphenoid in the *Macrognathus* species, and in *Mastacembelus pancalus* and *M. zebrinus* (Figs 27 & 28) stands in marked contrast to that in *Chaudhuria* and *Pillaia.* Except for its posterior tip, the parasphenoid is undivided, and its ventral surface is excavated into the form of a 'blind' pit from which the posterior portion of the large *adductor hyomandibulae* muscles originate. The cavity is particularly deep in *M. zebrinus* and *M. pancalus.* These species also differ in having a deep ventral ridge on the parasphenoid. This ridge lies medially along the posteroventral surface of the bone and divides the pit-like cavity; it is deepest in *M. zebrinus.*

The two ascending processes on the posterodorsal edge of the *1st infraorbital* bone (Fig. 3) are generally well-developed in all species. The posterior process articulates syndesmotically with the lateral ethmoid and may protrude posterodorsally in some species (Fig. 41a)

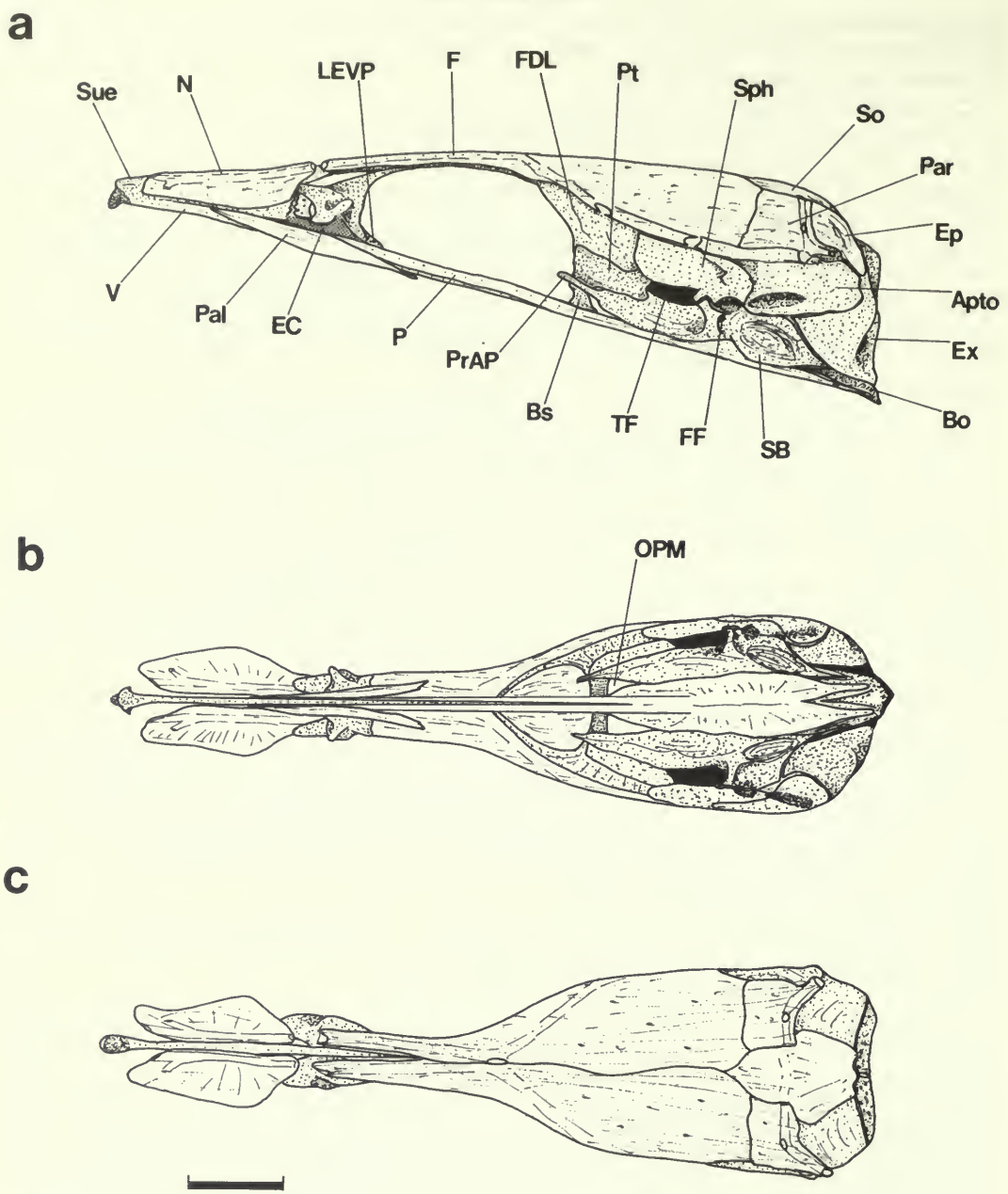


Fig. 26 *Mastacembelus maculatus* neurocranium in (a) lateral view left side, (b) ventral view and (c) dorsal view.

in association with the anterior expansion of the *adductor arcus palatini* muscle (discussed below p. 126). The shorter, anterior ascending process is absent in *Mastacembelus sinensis, Chaudhuria* and *Pillaia.* In these taxa, anterior to the posterior nasal opening the dorsal edge of the 1st infraorbital is straight and is connected by the integument to the nasal.

The posteroventral process or preorbital spine on the 1st infraorbital varies in its degree of development.

A preorbital spine (similar to that described in *M. mastacembelus* p. 16), occurs in the

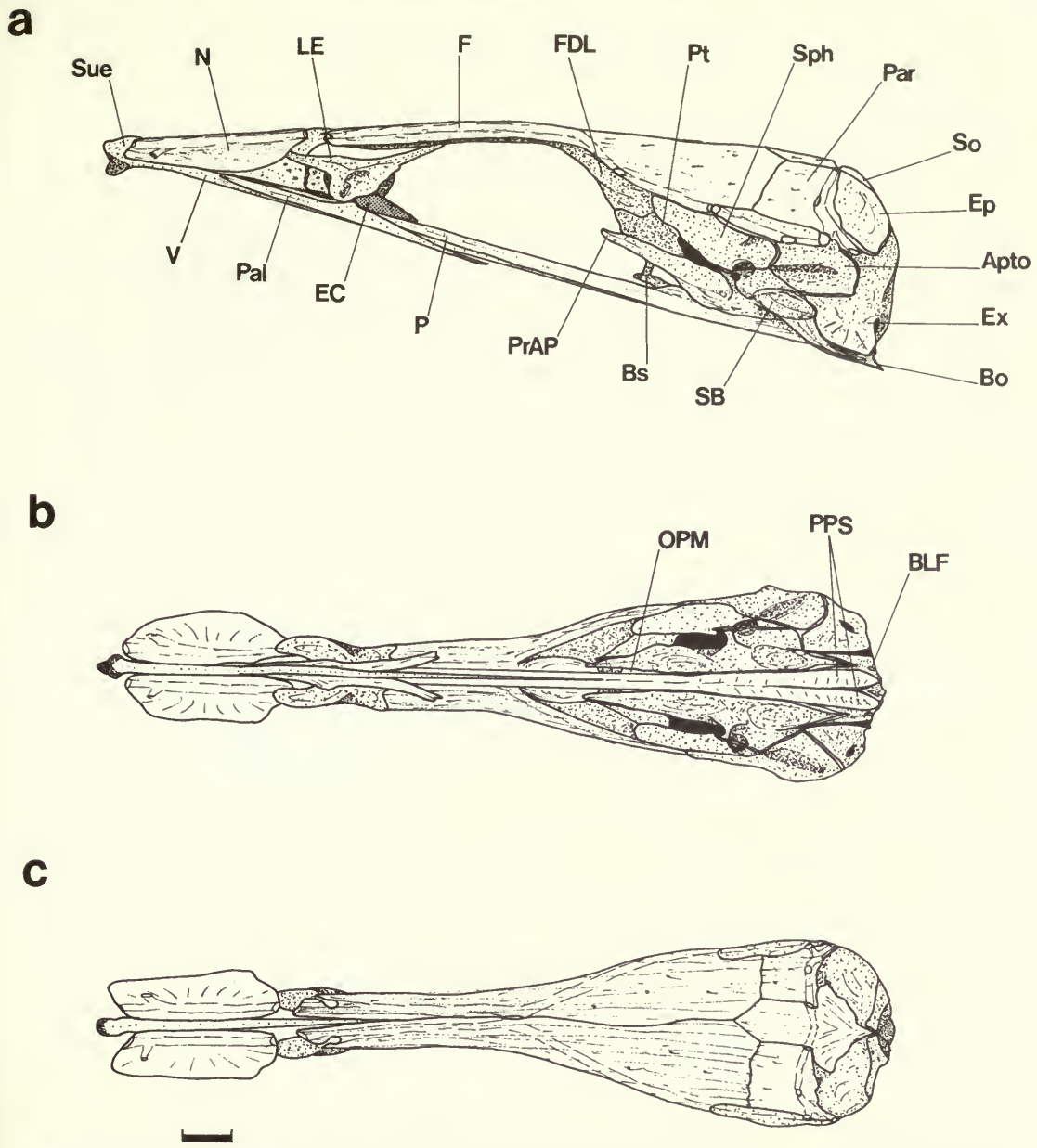


Fig. 27 *Mastacembelus zebrinus,* neurocranium in (a) lateral view, left side, (b) ventral view and (c) dorsal view.

majority of Asian species, it is absent in *Chaudhuria* (Fig. 15aiii) and *Pillaia* (Fig. 15biii) and is represented by a short posterior projection in *Macrognathus* (Fig. 41a). A spine is also well-developed in the majority of African mastacembeloids. In a number of species, however, (e.g. *Mastacembelus albomaculatus,* Fig. 41b) the spine is present only as a slight projection on the posteroventral edge of the 1st infraorbital and in others it is absent (e.g. *Mastacembelus aviceps* and *M. ophidium,* Fig. 41c & d). Intraspecific variation in the morphology of the preorbital spine in *Mastacembelus moorii* has been discussed by Matthes (1962: 73). He found a sequential development from a prominent spine in a juvenile

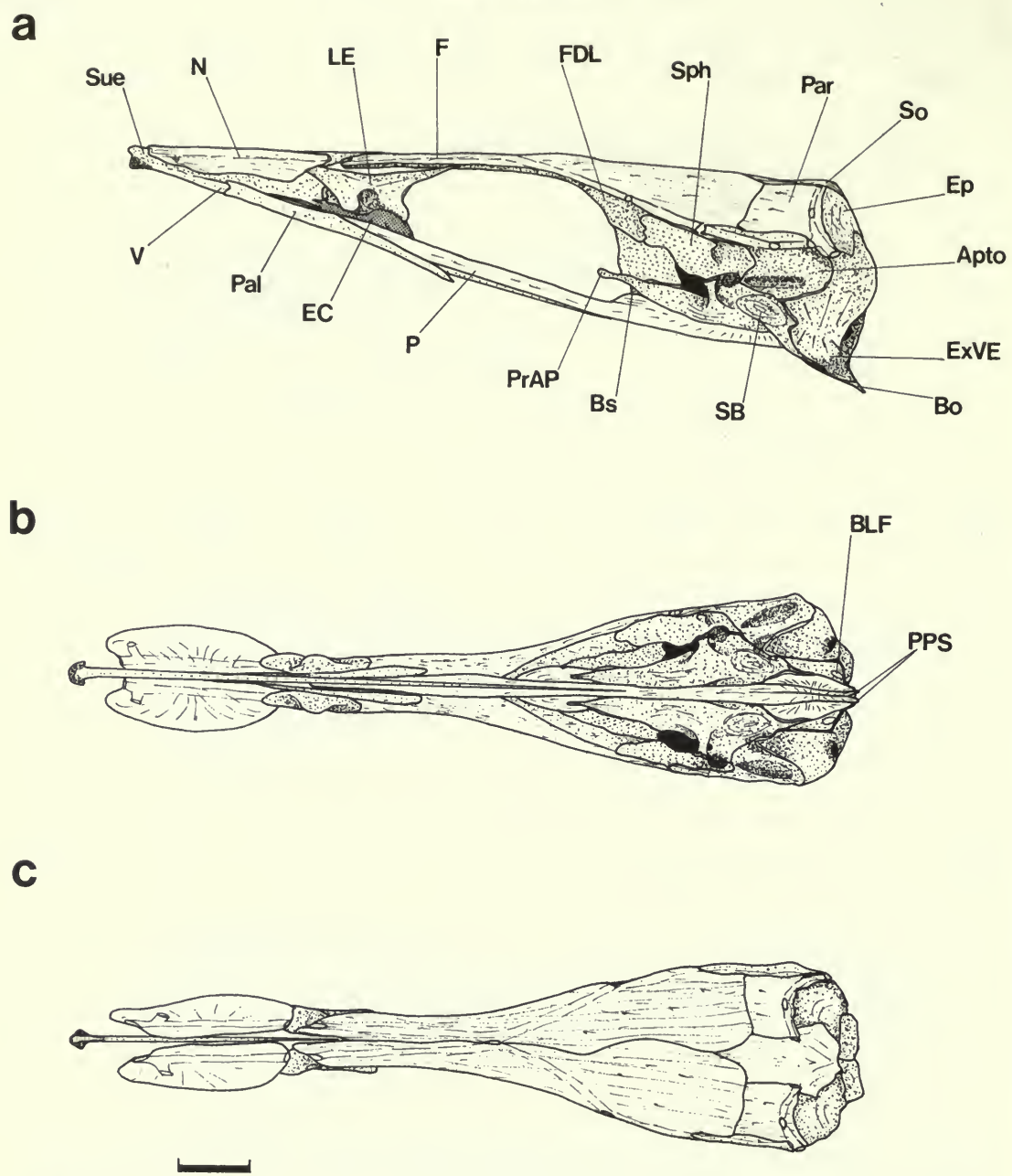


Fig. 28 *Mastacembelus pancalus,* neurocranium in (a) lateral view, left side, (b) ventral view and (c) dorsal view.

specimen (100 mm. long) to a much broader flange with only a slight projection on the posterodorsal corner in an adult specimen (410 mm. long).

If a prominent 1st infraorbital spine is absent in the adult, it was not found in pre-adult specimens of any species examined.

The remaining infraorbital bones are reduced to ossifications around the sensory canal. The extent to which the canal is ossified shows interspecific variation. In some African species

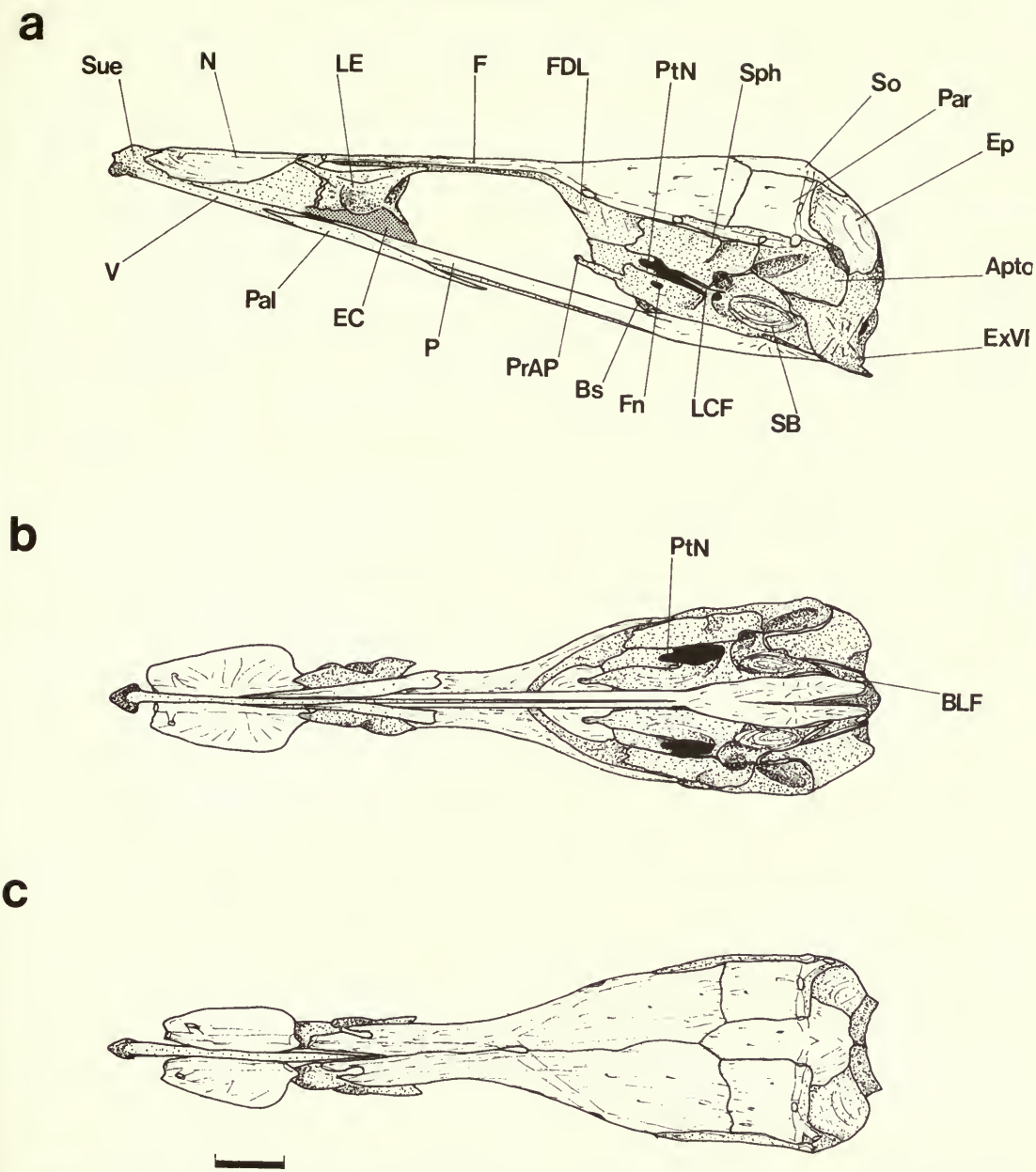


Fig. 29 *Macrognathus siamensis*, neurocranium in (a) lateral view, left side, (b) ventral view and (c) dorsal view.

(e.g. *Mastacembelus cunningtoni,* and *M. frenatus*) the canal is ossified along its entire length, and there are five infraorbital tubules, as in *M. mastacembelus* (p. 16). In contrast some taxa from Asia (e.g. *Chaudhuria* and *Pillaia*) and from Africa (*e.g. Mastacembelus brichardi*) have only the 1st element ossified. Between these extremes there is a series, incorporating the majority of mastacembeloid taxa, in which 1, 2, 3 or 4 tubules are ossified.

Otic region

The bones of the otic region show considerable interspecific variation in their morphology and will be considered individually.

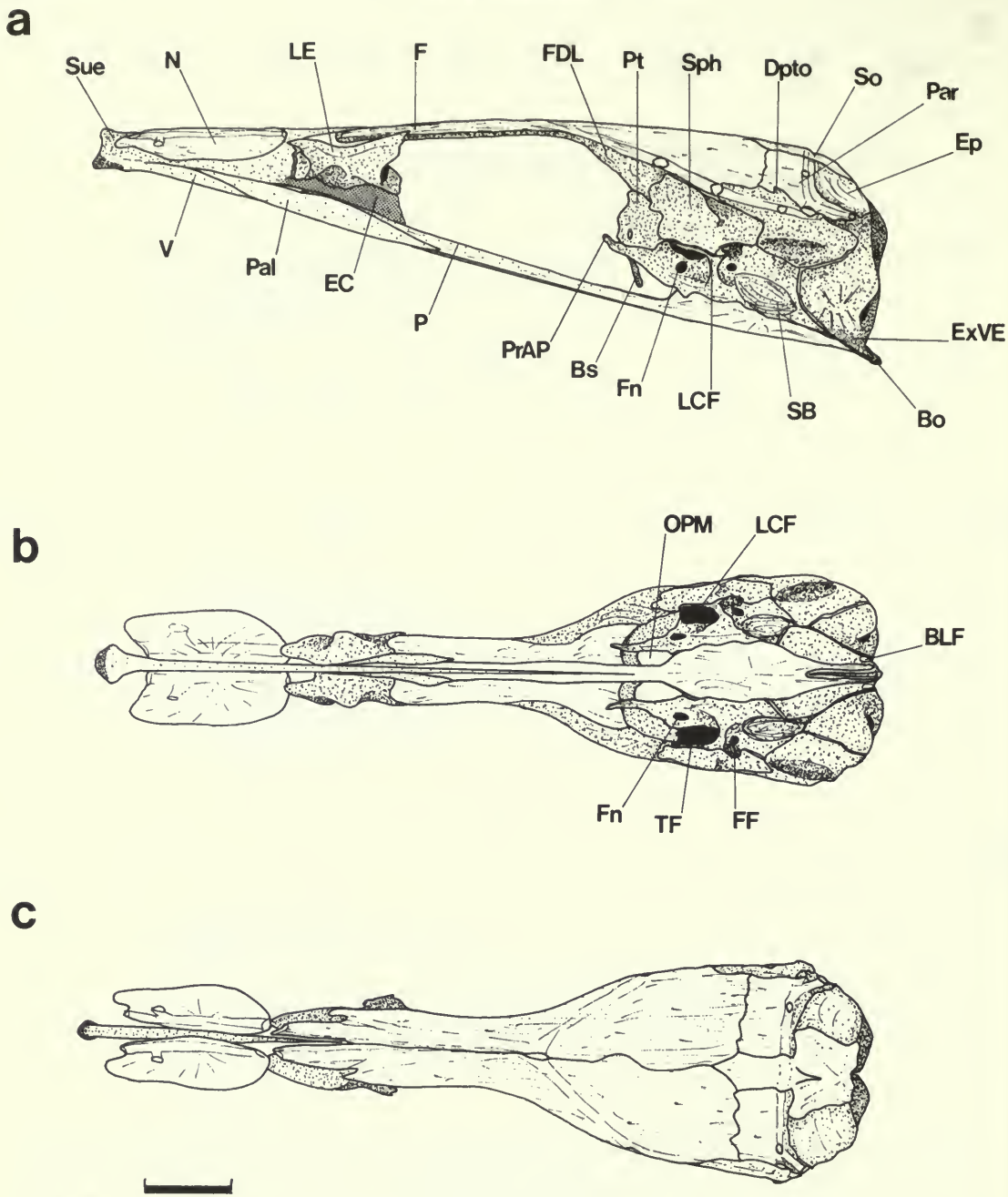


Fig. 30 *Macrognathus aculeatus,* neurocranium in (a) lateral view, left side, (b) ventral view and (c) dorsal view.

The otic region in all mastacembeloids is dominated by a particularly large *prootic* which, together with the sphenotic, pterosphenoid and descending frontal lamina forms the exceptionally long precommissural lateral wall of the neurocranium. The prootic is a long bone with a prominent anterior process in Asian and African species, although among the latter, there are 5 species which do not have the prootic developed to an extent comparable with

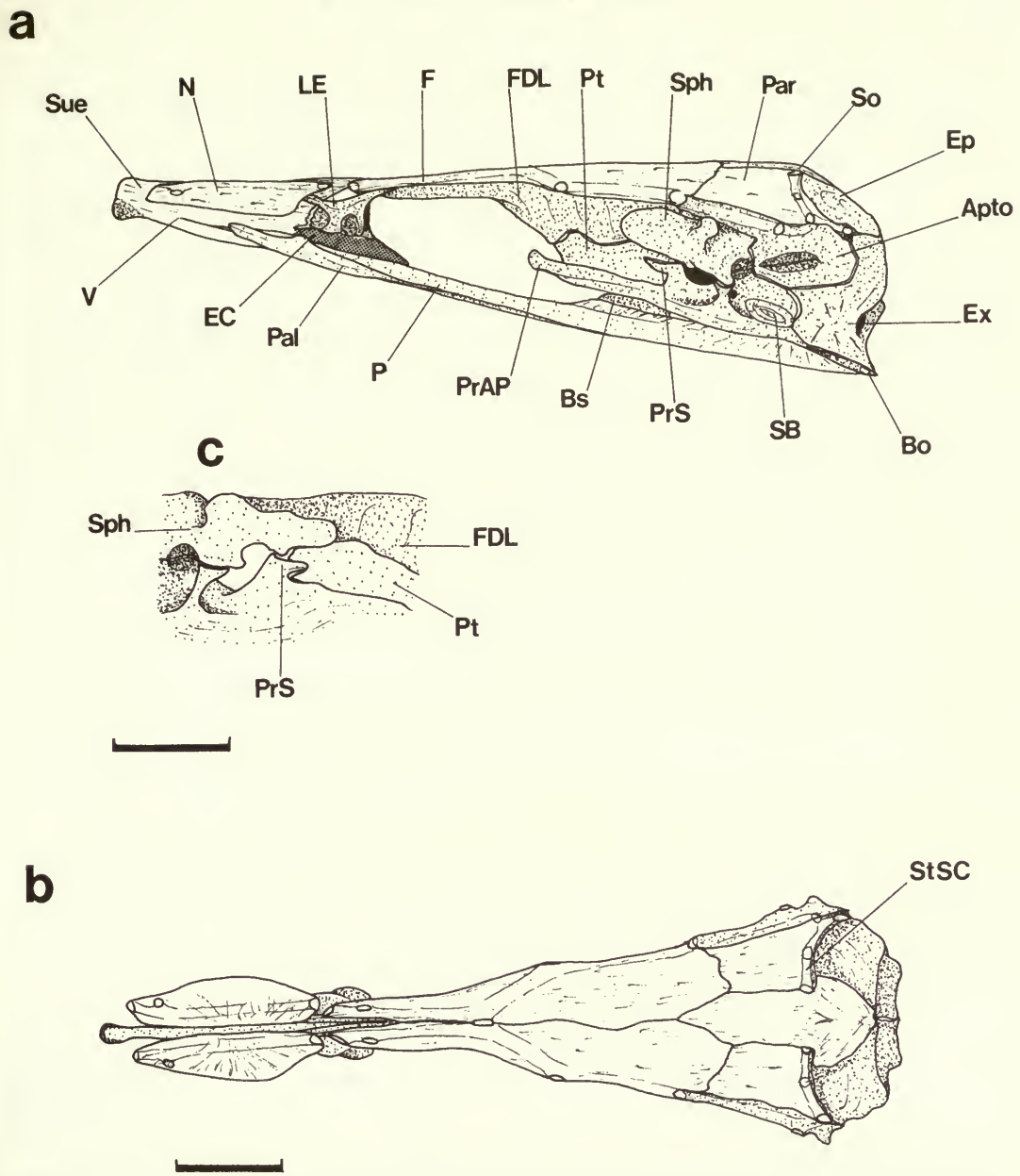


Fig. 31 *Mastacembelus frenatus,* neurocranium in (a) lateral view, left side and (b) dorsal view, and *Mastacembelus shiranus,* otic region (c) in lateral view, right side.

that of *M. mastacembelus.* In *Mastacembelus micropectus, M. brichardi* (Fig. 38a) and *M. longicauda* (Fig. 33a) the anterior prootic process extends only halfway across the lateral face of the pterosphenoid.

The condition in *Mastacembelus crassus* and *M. aviceps* (Figs 38a & 40a) is even more extremely modified. In these two crypto- and microphthalmic species the prootic anterior process is poorly developed, particularly in *Mastacembelus aviceps,* and extends only slightly anterior to the trigeminal foramen, this region of the neurocranium having a tubular shape.

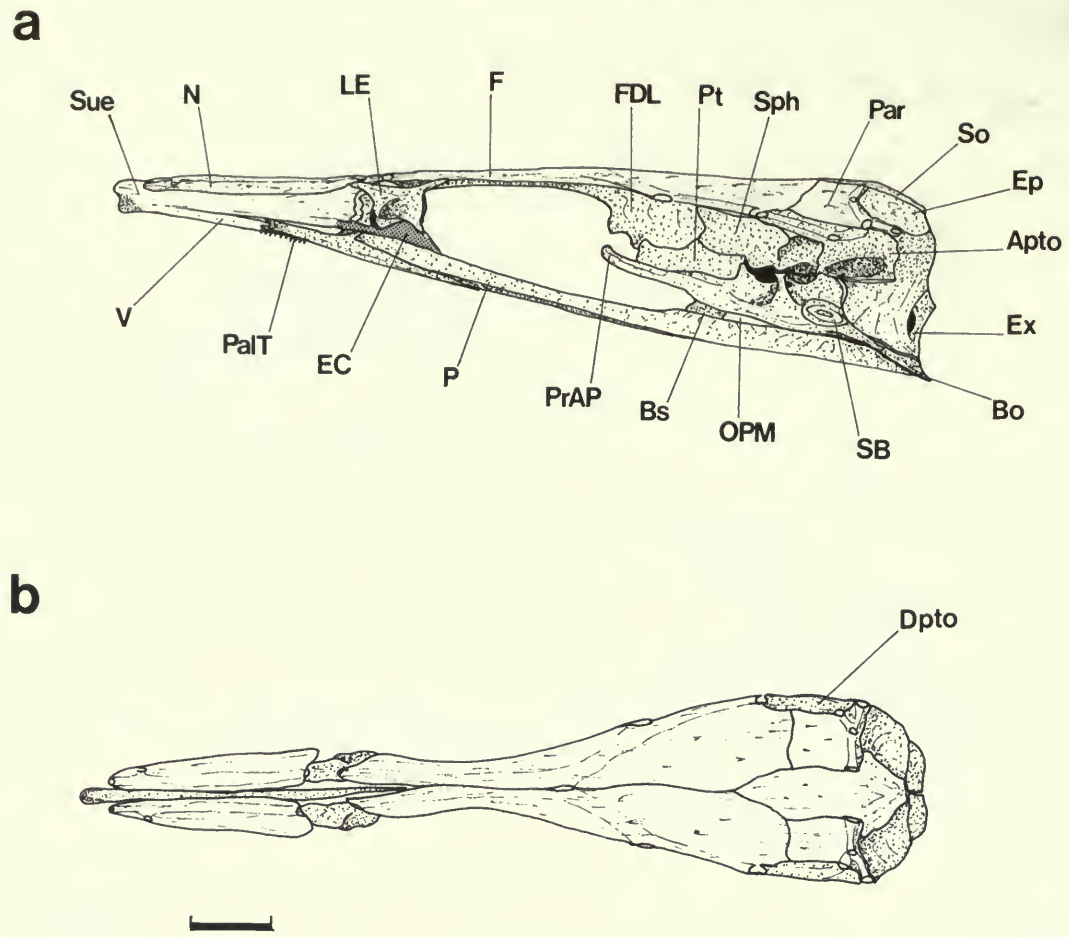


Fig. 32 *Mastacembelus congicus,* neurocranium in (a) lateral view, left side and (b) dorsal view.

Tubular neurocrania have been associated by Rosen & Greenwood (1976: 45) with eye reduction.

Among the Asian mastacembeloids, including those of the Middle East, *Pillaia* is the only taxon lacking a distinct anterior process on the prootic (Fig. 15bi). In *Pillaia,* as in *Mastacembelus aviceps,* the prootic does not extend anteriorly beyond the trigeminal foramen, and its overall tubular neurocranium can probably be correlated with its eye reduction.

In contrast to the arrangement in *M. mastacembelus* (Fig. 1a), the tip of the anterior process on the prootic in some species is curved anterodorsally and contacts a pedicel on the frontal and/or pterosphenoid. In these species the prootic bridges the nerves and blood vessels that emerge from the trigeminal foramen. A prootic bridge of this type was only found in 6 African taxa, *viz., Mastacembelus albomaculatus, M. moorii, M. plagiostomus* and *M. tanganicae,* all endemic to Lake Tanganyika, in *M. paucispinis* from the lower Zairean rapids, and in an undescribed *Mastacembelus* species recently collected by T. Roberts (pers. comm.) from the Cross River rapids in Cameroon.

The tip of the anterior process on the prootic is curved dorsally in *M. paucispinis* and *M. moorii* (Fig. 35 a & d) and contacts a wide pedicel on the lateral face of the descending frontal lamina. The *truncus supraorbitalis* and the internal jugular vein pass medial to the connection between these elements. A similar arrangement occurs in the undescribed species

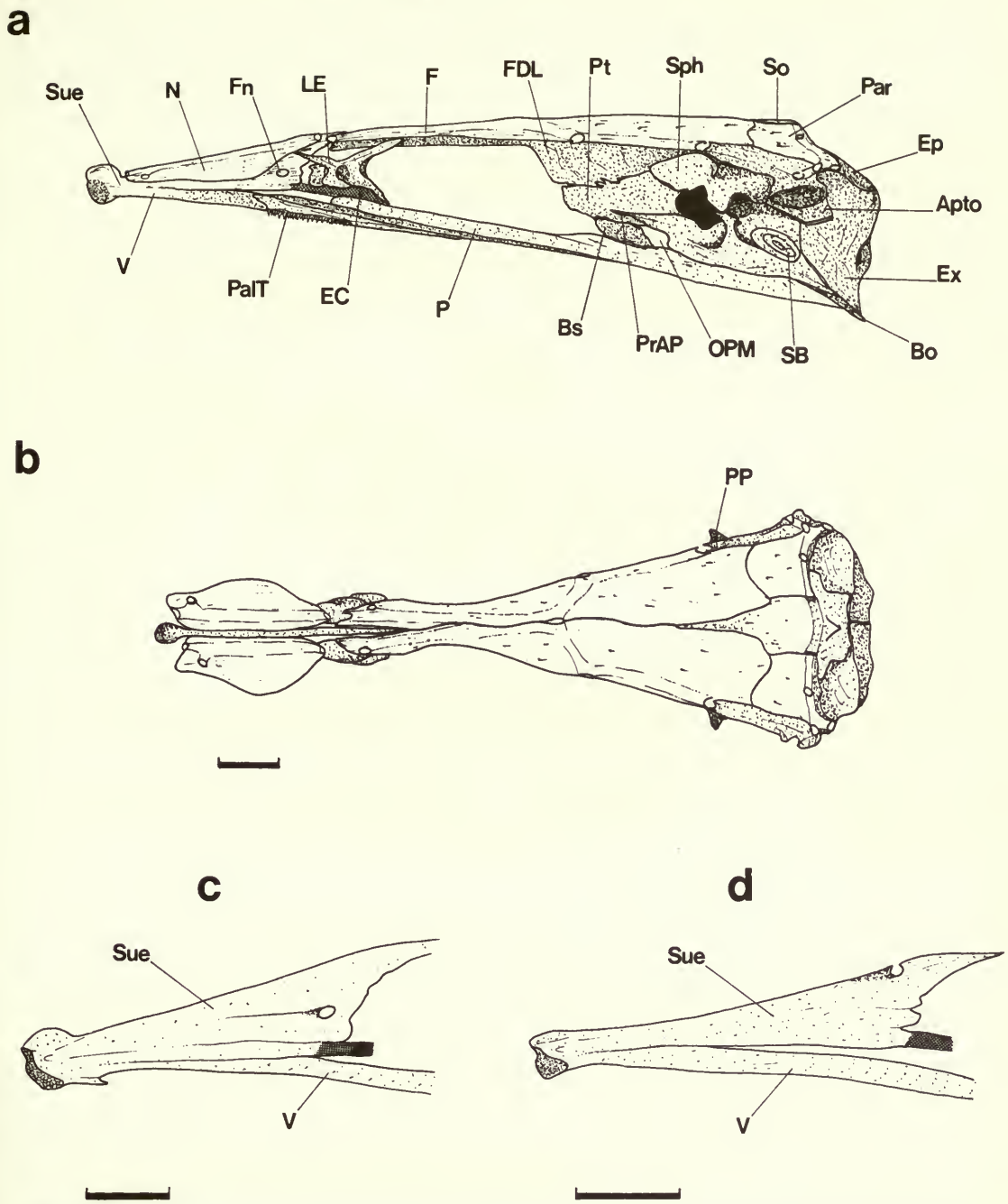


Fig. 33 *Mastacembelus longicauda,* neurocranium in (a) lateral view, left side, and (b) dorsal view, and *Mastacembelus reticulatus* (c), and *Mastacembelus sclateri* (d), ethmoid region in lateral view, left side.

(Fig. 36a). In that species the elements are not in direct contact but are joined by a short ligament. The tip of the anterior process on the prootic in *M. albomaculatus* and *M. plagiostomus* (Fig. 35c & f) forms a similar bridge across the anterolateral wall of the neurocranium by contacting a small pedicel on the pterosphenoid. In *M. tanganicae* (Fig.

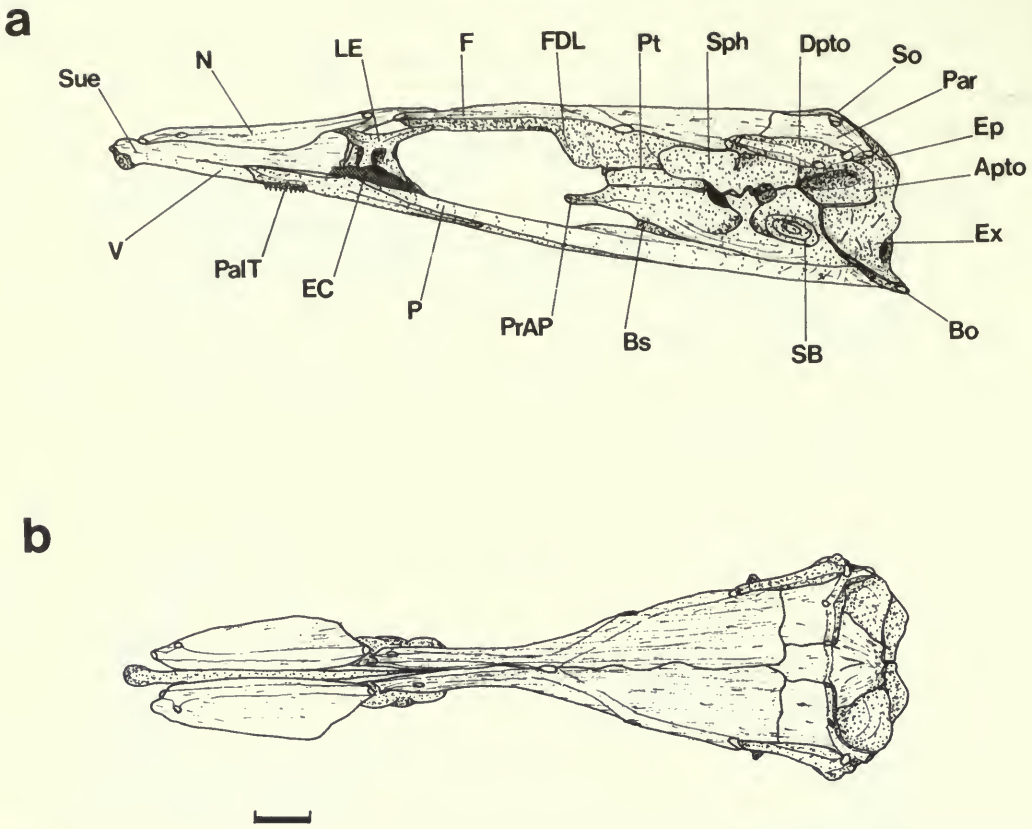


Fig. 34 *Mastacembelus nigromarginatus,* neurocranium in (a) lateral view, left side and (b) dorsal view.

35g) a bridge is present but results from the tip of the anterior process on the prootic curving posterodorsally to lie across the frontal/pterosphenoid lateral border.

Some variability found in the bridge of one specimen of *M. moorii* and one of *M. paucispinis* is not thought to represent significant intraspecific variation since the incomplete bridge on one side of the neurocranium in both these specimens appears to be the result of incomplete ossification at the tip of the anterior prootic process.

The tip of the anterior process is shaped like a hockey stick in the Zairean species *Mastacembelus ubangensis,* in *M. congicus* (Fig. 32a), and in the widely distributed *M. frenatus* (Fig. 31a). In these species the broad, slightly upturned tip of the prootic lies below a horizontal region on the ventral edge of the descending frontal lamina. A long ligament connecting the elements to form a bridge across the *truncus supraorbitalis* and the internal jugular vein, may be interpreted as an intermediate stage in the development of the bridge found, for example, in *M. paucispinis.*

A horizontal shelf-like ridge lies, longitudinally along the prootic, with its dorsal surface sloping ventrally, in 5 African species; *Mastacembelus moorii* and *M. zebratus* from Lake Tanganyika, *M. stappersii* from Zaire, *M. vanderwaali* from southern Africa (Skelton, 1976), and *M. sclateri* from Equatorial Guinea. A prootic 'shelf' is best developed in *M. sclateri* (Fig. 42a).

Here, and to a lesser extent in *M. stappersii* (Fig. 42b), it is continuous with the lower edge of a groove in the ventrolateral face of the pterosphenoid.

In *M. vanderwaali* the 'shelf' is in the form of a narrow ridge on the anterolateral face of the prootic and may represent a less derived condition than that described above. It

resembles the ridge on the anterolateral face of the prootic in *M. mastacembelus* (Fig. 1a, p. 17). *Mastacembelus moorii* has a short, horizontal 'shelf' on the midlateral face of the prootic. The lateral edge of this 'shelf' is inclined dorsally, giving it an up-turned edge affording greater support for the *truncus supraorbitalis* nerve and the internal jugular vein which pass longitudinally along its dorsal surface.

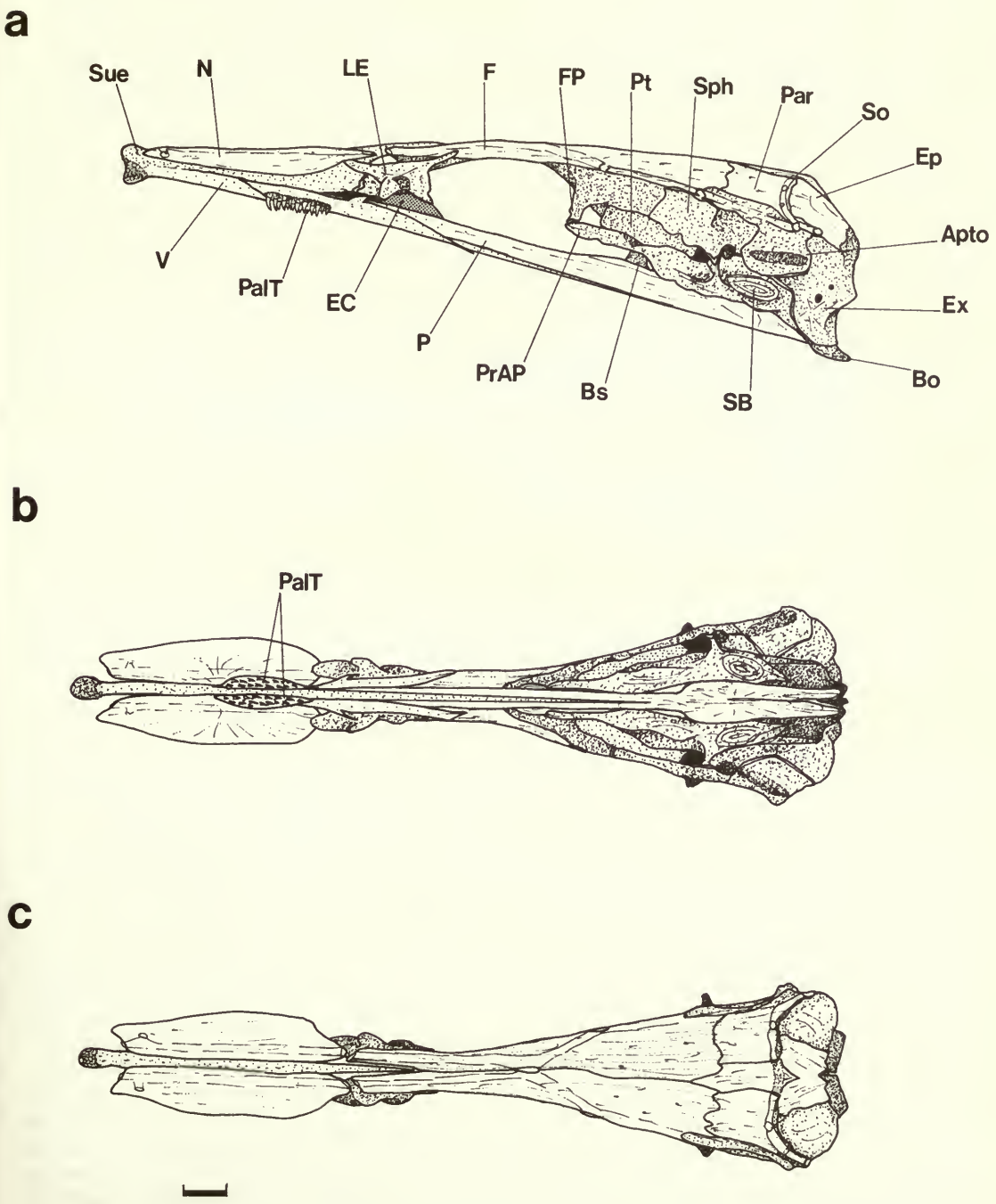


Fig. 35 a–c *Mastacembelus paucispinis* neurocranium. See p. 64 for full caption.

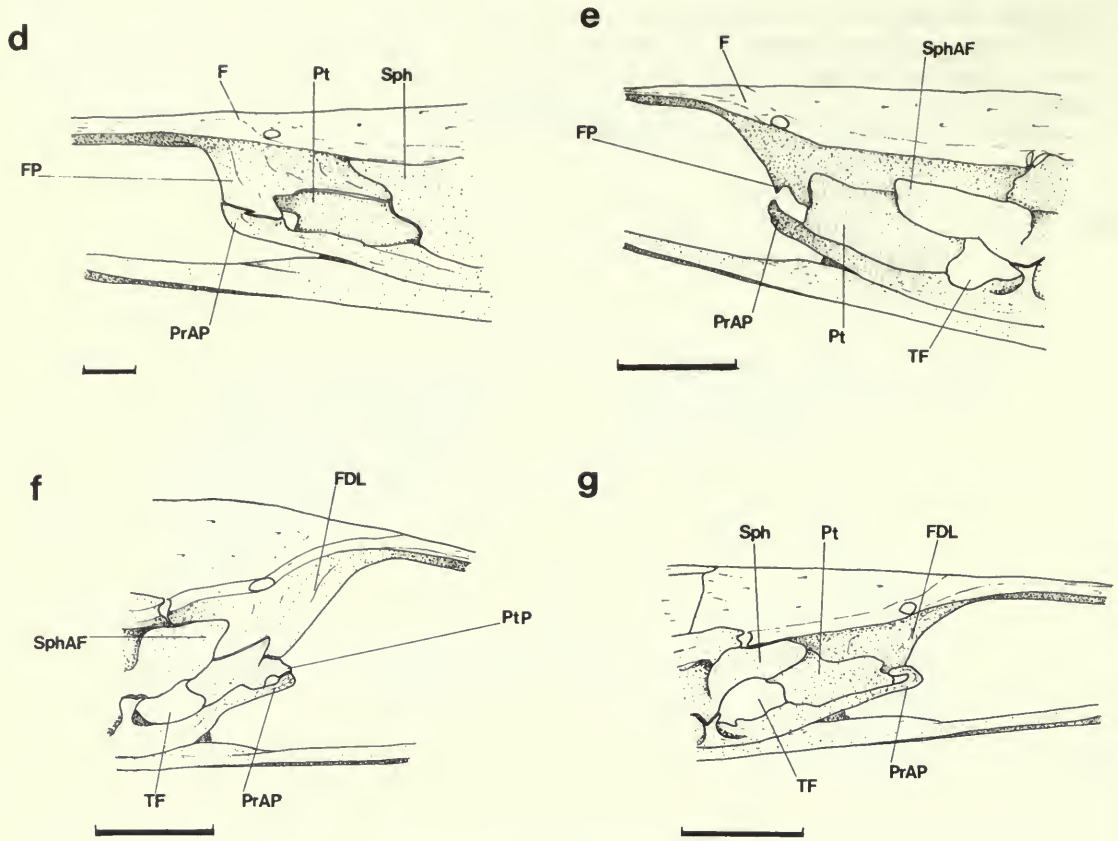


Fig. 35 *Mastacembelus paucispinis,* neurocranium in (a) lateral view, left side, (b) ventral view and (c) dorsal view. Also shown in lateral view is the pre-otic region in (d) *Mastacembelus moorii* and (e) *Mastacembelus albomaculatus* (left side), and (f) *Mastacembelus plagiostomus* and (g) *Mastacembelus tanganicae* (right side). See p. 63 for a–c.

A fenestra between the anterior process and the trigeminofacialis chamber pierces the lateral face of the prootic in the *Macrognathus* species (Figs 29a & 30a) and appears to be covered by a thin membrane.

The trigeminal foramen shows little interspecific variation in either its overall size or its position in the lateral wall of the neurocranium. However, the prootic spur which forms the anterior rim of the trigeminal foramen in *M. mastacembelus* (Fig. 1a) varies interspecifically in size and shape. When present, the tip of this spur may contact the ventral tip of a similar descending sphenotic spur in some Asian (e.g. *Mastacembelus armatus*) and African, (e.g. *Mastacembelus moorii*) mastacembeloids. In this condition, the posterior edge of the spur forms the anterior rim of the trigeminal foramen. The tips of the prootic and sphenotic spurs in other species (e.g. *Mastacembelus mastacembelus* and *M. vanderwaali*) do not always contact each other; instead, the posterior edge of the pterosphenoid is intercalated between their tips and thus contributes to the rim of the trigeminal foramen.

The ascending prootic spur in *Mastacembelus frenatus* (Fig. 31a) and in *M. shiranus* (from Lake Malawi, Fig. 31c) is particularly well-developed. In these species the tip is expanded, giving it in lateral view the shape of a cobbler's last. Apart from *M. frenatus, M. moorii* and *M. ophidium,* all Tanganyikan species lack a prootic ascending spur. This is also true of *M. brichardi, M. aviceps* and *M. brachyrhinus* from the Zairean rapids and *M. liberiensis, M. loennbergii, M. longicauda* and *M. sclateri* from Western Africa. In all African and Asian

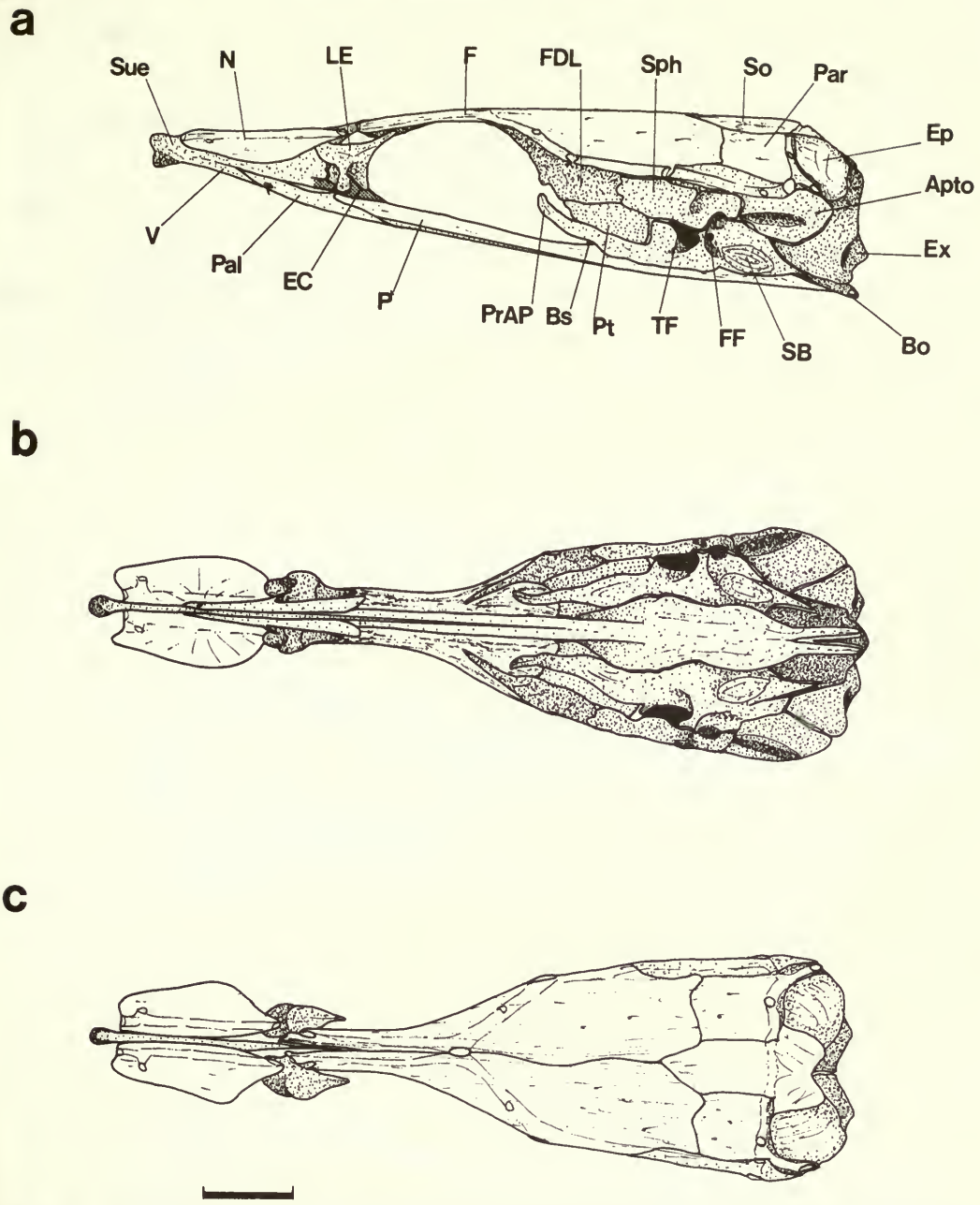


Fig. 36 Neurocranium of an undescribed *Mastacembelus* species in (a) lateral view, left side, (b) ventral view and (c) dorsal view.

species lacking a prootic ascending spur, the posterior edge of the pterosphenoid forms the anterior margin of the trigeminal foramen.

The prootic spur in *Macrognathus siamensis* (Fig. 29a) and *Macrognathus aral* is small. The posterolateral margin of the pterosphenoid is deeply notched in these species, and forms the anterior region of the trigeminal foramen.

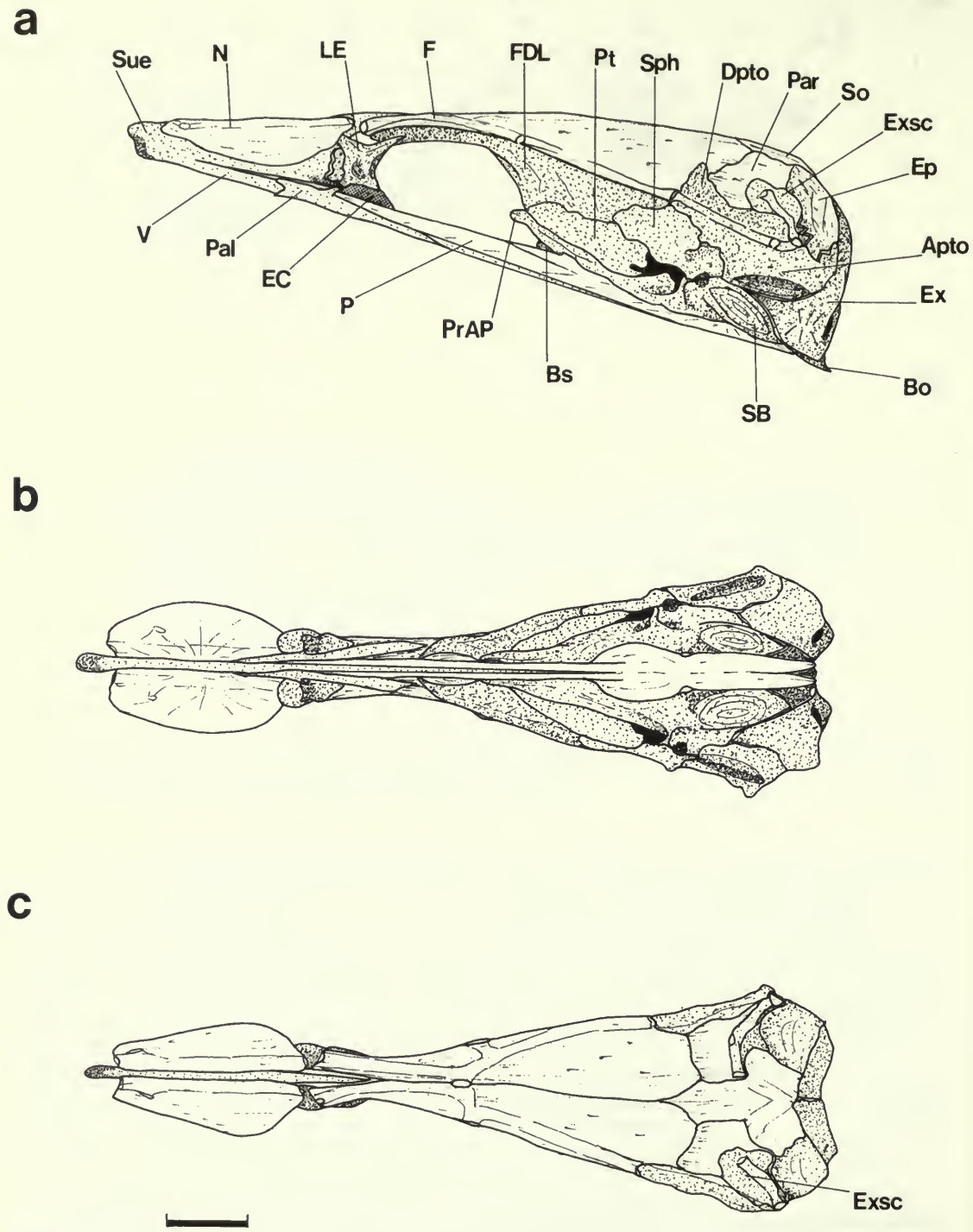


Fig. 37 *Mastacembelus brachyrhinus*, neurocranium in (a) lateral view, left side, (b) ventral view and (c) dorsal view.

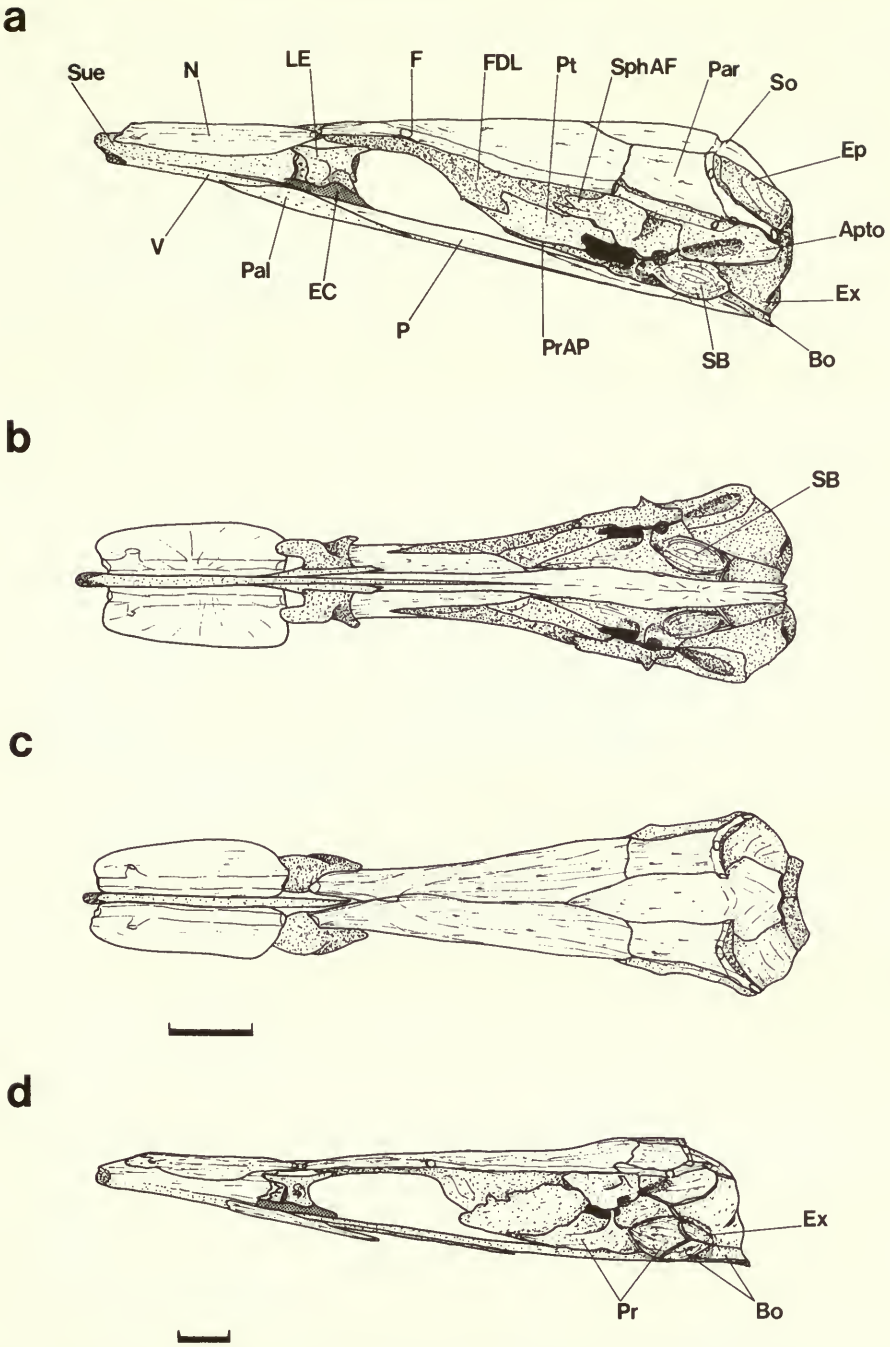


Fig. 38 Neurocranium of *Mastacembelus brichardi* in (a) lateral view, left side, (b) ventral view, (c) dorsal view; and of *Mastacembelus micropectus* (d) lateral view, left side.

The facial foramen in *Mastacembelus longicauda* (Fig. 33a) is unusually large and is connected, *via* a narrow opening, to the posterior margin of the trigeminal foramen. *Chaudhuria,* (Fig. 15ai), *Pillaia* (Fig. 15bi) and *Mastacembelus crassus* (Fig. 39a) lack separate trigeminal and facial foramina, and have a single large foramen in the trigeminofacialis chamber. An

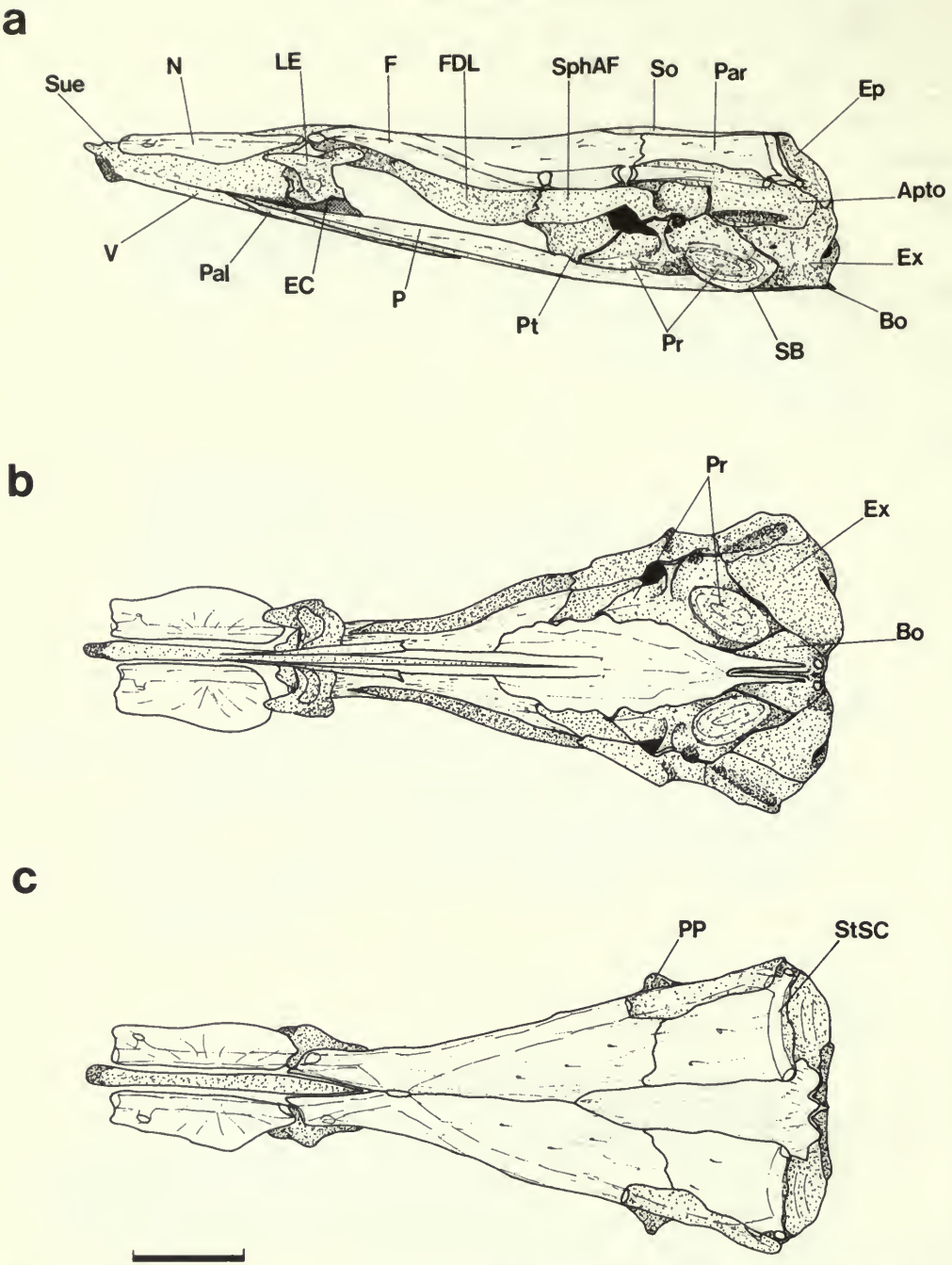


Fig. 39 *Mastacembelus crassus,* neurocranium in (a) lateral view, left side, (b) ventral view and (c) dorsal view.

even more extreme condition is found in *M. aviceps* where, due to the open postorbital lateral wall of the neurocranium, there are no foramina (Fig. 40a).

Interspecific variation in the size and position of the lateral commissure is slight apart from the development of an anterodorsal flange in some taxa. A flange on the anterodorsal face of the lateral commissure in *Macrognathus* is developed to an increasing degree in *M.*

siamensis (Fig. 29a), *M. aral* and *M. aculeatus*. In *M. aral* and *M. aculeatus* it extends anterolaterally to such an extent that in its most extreme condition (i.e. *M. aculeatus* Fig. 30a) it lies above the upper edge of the trigeminal foramen, and is sutured to the entire, precommissural ventral edge of the sphenotic.

A small sacculus lodged in the posteromedial face of the prootic (Fig. 1 a & b) is characteristic of most taxa. The bulla accommodating the sacculus in *M. brichardi* (Fig. 38 a & b), *M. crassus* (Fig. 39a & b) and *M. aviceps* (Fig. 40 a & b) is particularly large relative to the recess in *M. mastacembelus*. However, this otolith recess, regardless of its size, is accommodated entirely within the prootic in these species, as it is in the majority of mastacembeloids examined. A large bulla also occurs in *Mastacembelus micropectus* (Fig. 38d), *Chaudhuria* (Fig. 15ai & ii) and *Pillaia* (Fig. 15bi & ii). In these taxa, however, it is not lodged entirely in the prootic, but lies partly in the prootic, exoccipital and basioccipital bones.

There is little interspecific variation in the morphology of the *sphenotic*. A prominent anterolateral flange occurs in all taxa. This extension of the sphenotic, and the posterior position of its postorbital process, may be correlated with the long precommissural region of the neurocranium. The anterior edge of the sphenotic is sutured to the posterior edge of the frontal lamina (by which it is excluded from the postorbital border of the orbit) in most mastacembeloids. In *Chaudhuria* (Fig. 15ai) and *Pillaia* (Fig. 15bi) the anterior region is attenuated and, since the descending frontal lamina is absent, the tip passes to the posterior margin of the orbit. A similar condition occurs in *M. aviceps* (Fig. 40a) which also lacks a descending frontal lamina although in this species the sphenotic is shorter and does not extend anteriorly to the margin of the orbit. This arrangement is associated with the extreme precommissural attenuation of other neurocranial bones and a reduction in eye size.

The postorbital process on the sphenotic is developed to a varying extent. It is particularly large in the Tanganyikan species *Mastacembelus moorii* and *M. ophidium*, and in the west African species *M. goro* and *M. longicauda* (Fig. 33). In *Mastacembelus shiranus* the process is short, and it is absent in *M. vanderwaali*. When present this process serves as a point of insertion for the *levator arcus palatini* muscle (p. 119).

A ventrolateral 'wing' of the sphenotic occurs in *Mastacembelus congicus, M. niger, M. marmoratus, M. ubangensis, M. vanderwaali, M. goro, M. sclateri* and *M. nigromarginatus* (from Ghana; Fig. 34) and *M. reticulatus* (from Sierra Leone). It is particularly well developed in *M. congicus* (Fig. 32a) and overlies the trigeminal foramen to a greater extent than in any other species.

A small descending spur, like the prootic spur described above, on the ventral edge of the sphenotic occurs mosaically among the Asian and African species.

The most significant interspecific variation in the morphology of the *pterotic* occurs in a single Zairean species—*Mastacembelus brachyrhinus* (Fig. 37a & c). The dorsal (dermopterotic) part of the pterotic in this species is enlarged in comparison with its condition in *M. mastacembelus* (Fig. 1a & c), which latter condition represents the more usual mastacembeloid arrangement. The enlarged dorsal region of the pterotic in *M. brachyrhinus* is combined with a posterodorsal expansion of the frontal.

The condition of the *epioccipital* in *M. mastacembelus* (Fig. 1c) reflects the arrangement of this bone in both Asian and African mastacembeloids.

The *exoccipital* varies interspecifically in a number of features. Its dorsomedial process, as described in *M. mastacembelus* (p. 18), is not connected to its partner in *Mastacembelus sinensis* (Fig. 24c), *Chaudhuria* (Fig. 15aiii) or in *Pillaia* (Fig. 15biii). In these species the posterodorsal edge of the supraoccipital lies between the dorsomedial face of each exoccipital. The foramen magnum is not, therefore, surrounded by the exoccipitals alone but by the posterior edge of the supraoccipital as well. A further characteristic of the exoccipital in these three taxa is its perforated dorsal surface.

The ventrolateral face of the exoccipital is expanded in taxa with a deep basicranium (p. 53). In these, which include *Mastacembelus pancalus* (most extreme basicranial expansion), *Mastacembelus zebrinus* and to a lesser extent *Macrognathus*, the lateral wall of the

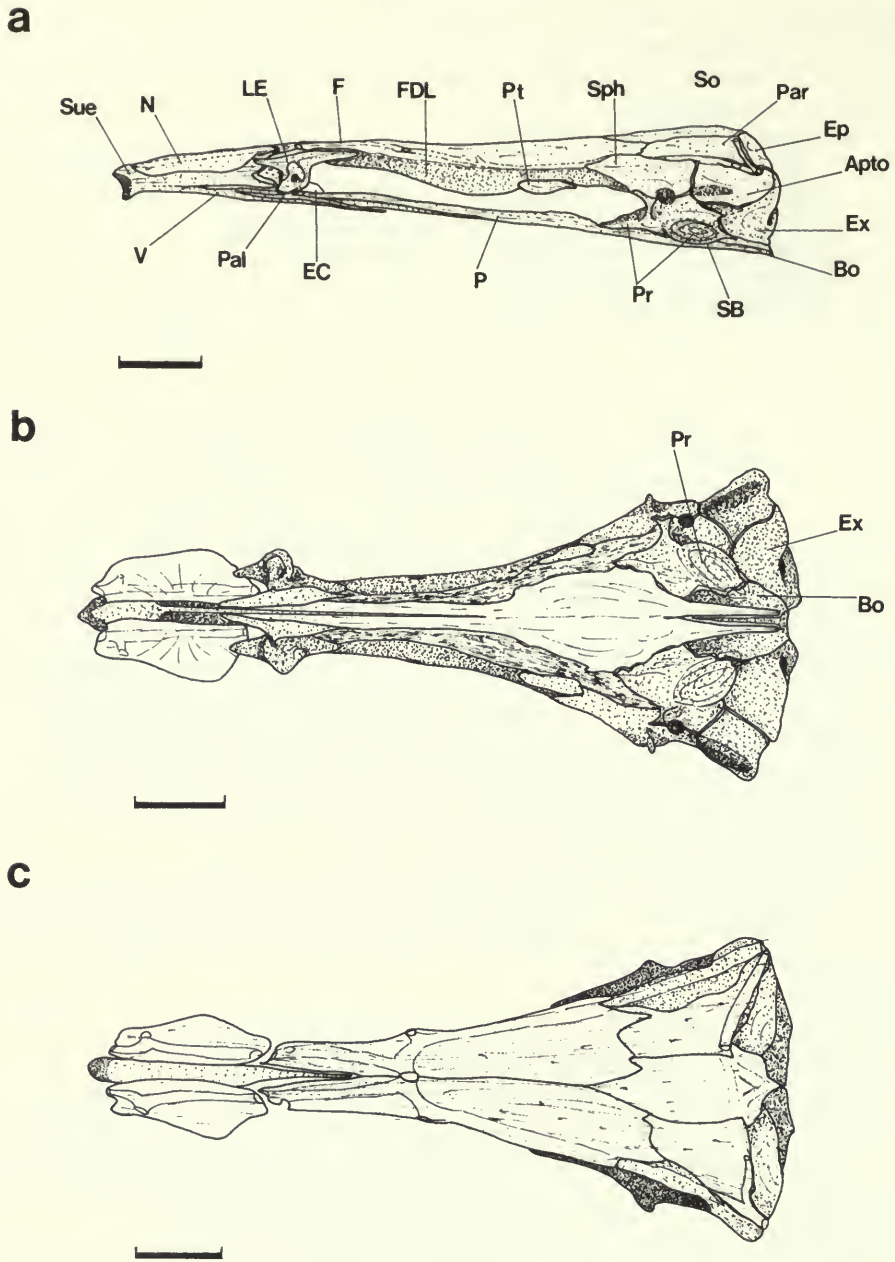


Fig. 40 *Mastacembelus aviceps,* neurocranium in (a) lateral view, left side, (b) ventral view and (c) dorsal view.

exoccipital is expanded ventrally and thus contributes to the deepening of the basicranium. The *basioccipital* also contributes to the overall increase in depth of the basicranium in *M. pancalus, M. zebrinus* and in *Macrognathus* species.

The expanded *basioccipital* in *M. pancalus* extends posteroventrally below the craniovertebral joint. The fossa for Baudelot's ligament is particularly deep in *M. pancalus* (Fig. 28b), it lies on the posteroventral edge of the basioccipital, and has an ovoid opening. The fossa is in a similar position in *M. zebrinus* and all the *Macrognathus* species.

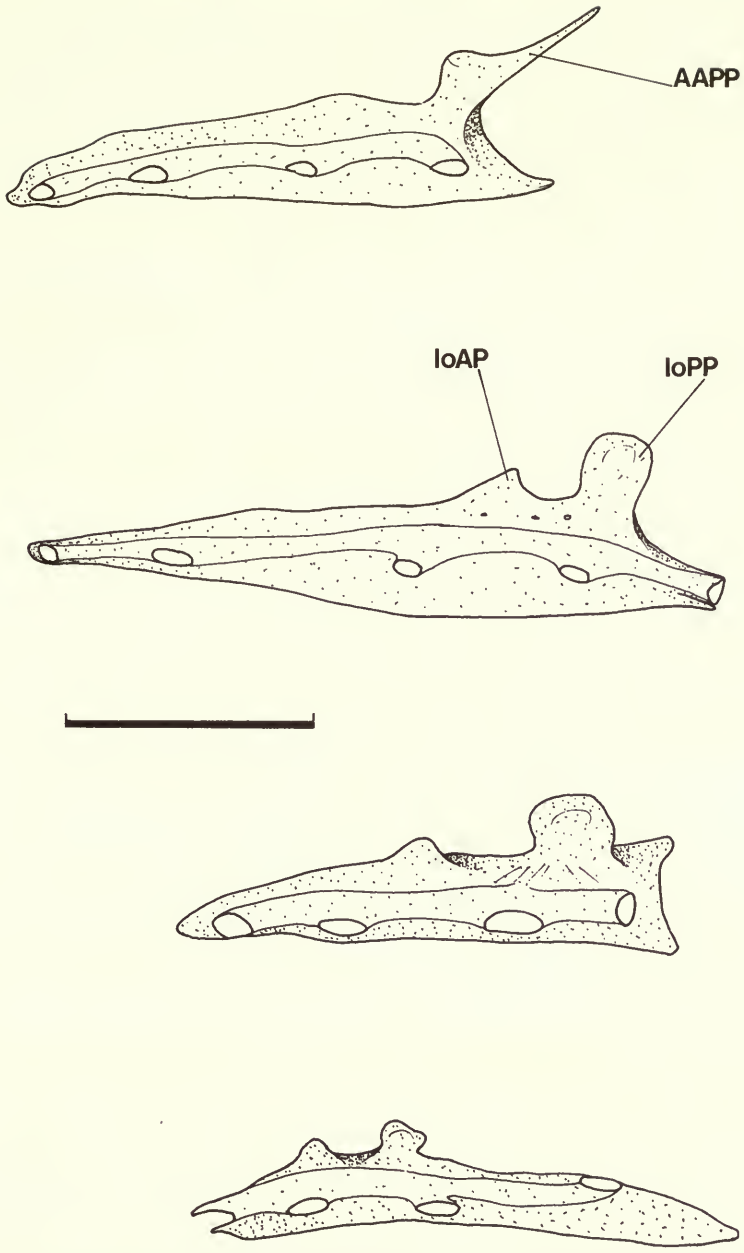


Fig. 41 Lateral view of left 1st infraorbital bone in (a) *Macrognathus aculeatus,* (b) *Mastacembelus albomaculatus,* (c) *Mastacembelus aviceps* and (d) *Mastacembelus ophidium* (right side).

A tripartite occipital facet, (p. 18) occurs in all mastacembeloids.

There is little interspecific variation in the morphology of the *supraoccipital,* apart from the extent to which it contributes to the dorsal rim of the foramen magnum (discussed above).

The supraoccipital is a comparatively small bone in *M. sinensis* (Fig. 24c) and may not contact the frontals anteriorly; as a result the anteromedial edge of the parietals contact medially.

The transverse channel that crosses the posterodorsal surface of the supraoccipital in *M. mastacembelus* (Fig. 1c) is absent in several Asian and African species. Among the Asian taxa, *Mastacembelus pancalus* (Fig. 28c), *M. sinensis* (Fig. 24c), *Chaudhuria* (Fig. 15aiii) and *Pillaia* (Fig. 15biii) all lack a channel; and it is also absent in *Mastacembelus albomaculatus, M. cunningtoni, M. frenatus* (Fig. 31c), *M. plagiostomus, M. tanganicae, M. zebratus, M. shiranus, M. congicus* (Fig. 32c), *M. aviceps* (Fig. 40c) and *M. ubangensis* among the African species. The sensory canal commissure in these African species lies within the integument above the dorsal surface of the supraoccipital.

A dermosupraoccipital, as described in *Mastacembelus congicus* by Taverne (1973), was not distinguished in any mastacembeloids examined, nor could I find any trace of the element Patterson (1977: 98) described as '... a plate-like median extrascapular which overlies the supraoccipital and may fuse with it in full grown individuals'.

The transverse channel across the dorsal surface of the supraoccipital, which accommodates the supratemporal sensory canal commissure, is covered by a thin layer of bone in some species (e.g. *Mastacembelus moorii*) and presumably results from the supraoccipital enclosing this canal during ontogeny.

The *extrascapulae,* both lateral and medial, are absent in all mastacembeloid taxa although my specimen of *Mastacembelus brachyrhinus* (Fig. 37c) is presumably exceptional as a left lateral extrascapula is clearly discernible.

The *frontal* shows interspecific variation in the morphology of its dorsal surface and its vertical lamina. In *M. mastacembelus* (Fig. 1a) and a number of other Asian species (e.g. *Mastacembelus erythrotaenia,* Fig. 25c), and the majority of African species (e.g. *Mastacembelus frenatus,* Fig. 31c) the dorsal surface of the frontal is almost flat, with only the lateral edge curved ventrally. A group of Asian taxa including *Mastacembelus pancalus, M. zebrinus* and the *Macrognathus* species have a frontal with a strongly curved dorsal surface. In *M. pancalus* (Fig. 28a) the lateral edge of the frontal is curved ventrally to such an extent that, in transverse section, the highest point on the dorsal surface of the neurocranium is along the median connection of the frontals. A similar type of frontal morphology occurs in *M. zebrinus* and to a lesser extent in the *Macrognathus* species. Its curvature in these species gives the neurocranium a much deeper appearance than that of *M. mastacembelus.* A further consequence of a steeply sloping frontal is the relatively ventral position of the trigeminofacialis chamber. Such a condition may also be correlated with the marked basicranial expansion in these taxa (as described earlier p. 69).

The dorsal surface of the frontal is curved to a varying degree in a number of other species (e.g. *Mastacembelus brachyrhinus* and *M. brichardi*), but no other Asian or African taxa exhibit the pronounced curvature of the frontal found in *M. pancalus, M. zebrinus* and in all *Macrognathus* species.

The anterior region of the frontal, which roofs the orbit, is short in *Mastacembelus brichardi* (Fig. 38c), *M. crassus* (Fig. 39c) and *M. aviceps* (Fig. 40c), and is apparently associated with the small eyes of these rapids-dwelling species (see also p. 125).

A descending vertical lamina on the frontal, as described in *M. mastacembelus* (p. 19) is a characteristic feature of all mastacembeloids apart from *Chaudhuria* (Fig. 15ai) and *Pillaia* (Fig. 15bi). The lack of a frontal lamina is one of many characters in the neurocranium of *Chaudhuria* and *Pillaia* that are possibly reductional. A comparatively low descending frontal lamina occurs in the highly derived taxa of the Zairean rapids, *Mastacembelus aviceps* (Fig. 40a) and *M. crassus* (Fig. 39a). Variability in the size of the lamina and the presence of a pedicel on its lateral face have been discussed above (p. 60).

There is little interspecific variation in the morphology of the *parietal.* The parietals in all Asian and African species apart from *Chaudhuria* (Fig. 15aiii) and *Pillaia* (Fig. 15biii) accommodate the supratemporal branch of the cephalic sensory canal system (Maheshwari, 1971), normally associated with the extrascapulae. A pore is present in the canal in all taxa except *Chaudhuria* and *Pillaia.* The medial connection between the parietals in *Mastacembelus sinensis* (Fig. 24c) is unique to that species, and is directly related to the small dorsal area of the supraoccipital (p. 71). The relatively small dorsal surface area of the parietal in

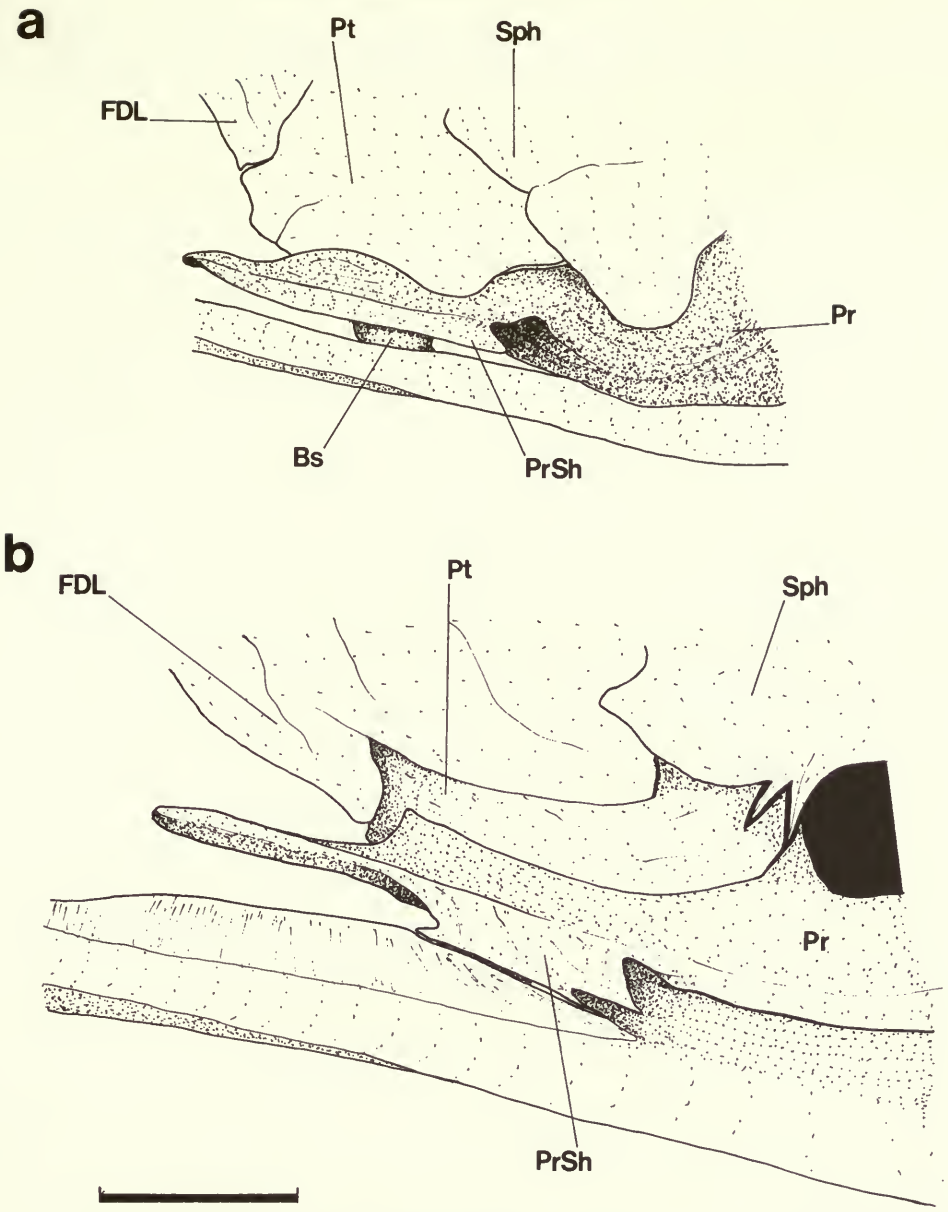


Fig. 42 Pre-otic region of neurocranium in (a) *Mastacembelus sclateri* and (b) *Mastacembelus stappersii*; lateral view, left side.

Mastacembelus brachyrhinus (Fig. 37c), in association with the enlarged pterotic and posterior region of the frontal (p. 69), is a characteristic of the species.

The absence of a *posttemporal* bone is a characteristic feature of all taxa. The only remnant of this bone in *M. mastacembelus* is two ossified tubules which surround two sections of the postcranial sensory canal (p. 19). Interspecific variation in the number of posttemporal tubules among Asian and African species is summarised in Table 4. Tubules are completely absent in some Asian (including *Mastacembelus armatus, M. sinensis, Chaudhuria* and *Pillaia*) and African taxa (including *Mastacembelus shiranus, M. congicus, M. brichardi, M. niger, M. sclateri* and *M. flavomarginatus*). Intraspecific variation in the number of tubules

Table 4 Number of posttemporal tubules in mastacembeloid species.

	Absent	1	2	3
Oriental mastacembeloid taxa				
Mastacembelus armatus	+			
Mastacembelus erythrotaenia			+	
Mastacembelus maculatus		+		
Mastacembelus mastacembelus			+	
Mastacembelus pancalus		+		
Mastacembelus sinensis	+			
Mastacembelus unicolor			+	
Mastacembelus zebrinus		+		
Macrognathus aculeatus		+		
Macrognathus siamensis		+		
Chaudhuria caudata	+			
Pillaia indica	+			
African mastacembeloid taxa				
Mastacembelus albomaculatus			+	
Mastacembelus aviceps			+	
Mastacembelus batesii			+	
Mastacembelus brachyrhinus			+	
Mastacembelus brevicauda			+	
Mastacembelus brichardi	+			
Mastacembelus congicus	+			
Mastacembelus crassus			+	
Mastacembelus cunningtoni			+	
Mastacembelus ellipsifer			+	
Mastacembelus flavomarginatus	+			
Mastacembelus frenatus			+ (L)	+ (R)
Mastacembelus goro		+		
Mastacembelus greshoffi			+	
Mastacembelus liberiensis			+	
Mastacembelus loennbergii			+	
Mastacembelus longicauda			+	
Mastacembelus marmoratus			+	
Mastacembelus micropectus			+	
Mastacembelus moorii			+	
Mastacembelus niger	+			
Mastacembelus nigromarginatus			+	
Mastacembelus ophidium		+ (R)		+ (L)
Mastacembelus paucispinis			+	
Mastacembelus plagiostomus				+
Mastacembelus platysoma			+	
Mastacembelus reticulatus			+ (L)	+ (R)
Mastacembelus sclateri	+			
Mastacembelus shiranus	+			
Mastacembelus stappersii			+	
Mastacembelus tanganicae			+	
Mastacembelus vanderwaali			+	
Mastacembelus zebratus				+
Mastacembelus sp. nov.			+	

may also occur. For example, one side of the head in a specimen of *M. frenatus* and one of *M. reticulatus,* has three and the other side two tubules, while a specimen of *M. ophidium* has three tubules on the left and only one of the right side.

Jaws

Upper jaw

There is little variation in the overall morphology of these bones. The most extreme variation occurs in *Pillaia* (Fig. 16b) where the upper jaw is formed from a single tooth bearing element. This bone was identified by Yazdani (1976*a*) as a *premaxilla*, and he suggested '... the posterior part of the upper jaw bone in *Pillaia indica* represents the maxilla which has fused with the premaxilla in the course of evolution ...'. The jaws in the specimens of *Pillaia* examined confirm that a single bone is present, but, whether this is the result of fusion or the loss of the *maxilla* cannot be determined without ontogenetic evidence.

The upper jaw arrangement in *Mastacembelus aviceps,* from the lower Zairean rapids, may help clarify this problem. The anterior half of the maxilla in *M. aviceps* (Fig. 44a) is reduced to an attentuated bony strand lying within a longitudinal groove on the dorsal surface of the premaxilla. Posteriorly, the maxilla is thickened and expanded ventrolaterally to a level below the premaxilla, with which bone it is tightly connected. These modifications in *M. aviceps* give its upper jaw a marked resemblance to that in *Pillaia.* This may be the result of a similar developmental trend in the two taxa, a trend which in *Pillaia* is at a more advanced stage and has involved the complete loss of the reduced anterior region of the maxilla and a fusion of the broader posterior flange to the premaxilla.

The anterior region of the maxilla is expanded in *Mastacembelus moorii* (Fig. 43a) and *M. ophidium* (Fig. 43b) from Lake Tanganyika. In these species the anterior half of the maxilla is lateromedially compressed, giving it a wide anterolateral face which may function as a support for the exceptionally large and fleshy lips.

The premaxillary dentition exhibits considerable variation in the size and number of teeth. Typically it consists of an outer row of large caniniform teeth followed by three of four inner rows which decrease in number and tooth size posteromedially, e.g. the Asian *Mastacembelus maculatus* and *M. armatus,* and the African *M. frenatus* and *M. goro.* Teeth in the outer row are particularly large in *Mastacembelus moorii* and *M. ophidium* (Fig. 43a & b) and there are numerous inner rows of small teeth. The dentition in these taxa gives the premaxilla a characteristically wide alveolar surface, possibly related to their piscivorous diet.

The alveolar surface on the premaxilla of a third Tanganyikan species, *Mastacembelus cunningtoni* (Fig. 45a) is wide, with up to eighteen irregular rows of small, slender teeth, each with a posteriorly curved tip. A broad alveolar surface on the premaxilla is also a feature of a number of Asian mastacembeloids, including *Mastacembelus zebrinus, M. pancalus* and the *Macrognathus* species (Fig. 46). In these taxa the rostral appendage is larger than in other mastacembeloids, and in *M. pancalus* (and to a lesser extent in *M. zebrinus*) the alveolar surface of the premaxilla is curved ventrorostrally around its buccal face. The under surface bears numerous, small, irregularly spaced caniniform teeth which tend to lie horizontally, their tips directed posteriorly. Anteriorly, the premaxillary alveolar surface contacts its partner in a symphysis anteroventral to the head of the vomer. Furthermore, the anterior tip of this tooth bearing surface has fragmented into a single plate on the right premaxilla in a specimen of *M. pancalus* (Fig. 45b).

The fragmentation of the alveolar surface in *Macrognathus* species appears to represent a more advanced stage in the phylogenetic development of this character from its condition in *Mastacembelus pancalus.* The anterior end of the alveolar surface in *Macrognathus* has fragmented into a long series of laterally expanded, flexible dentigerous bony plates (Fig. 45c) which extend along the ventral surface of the rostral appendage and are tapered anteriorly. The smallest plate lies posteroventral to the anterior nostril and the tip of the rostrum. On the ventral surface of each pair of rostral plates is a transverse row of small caniniform teeth

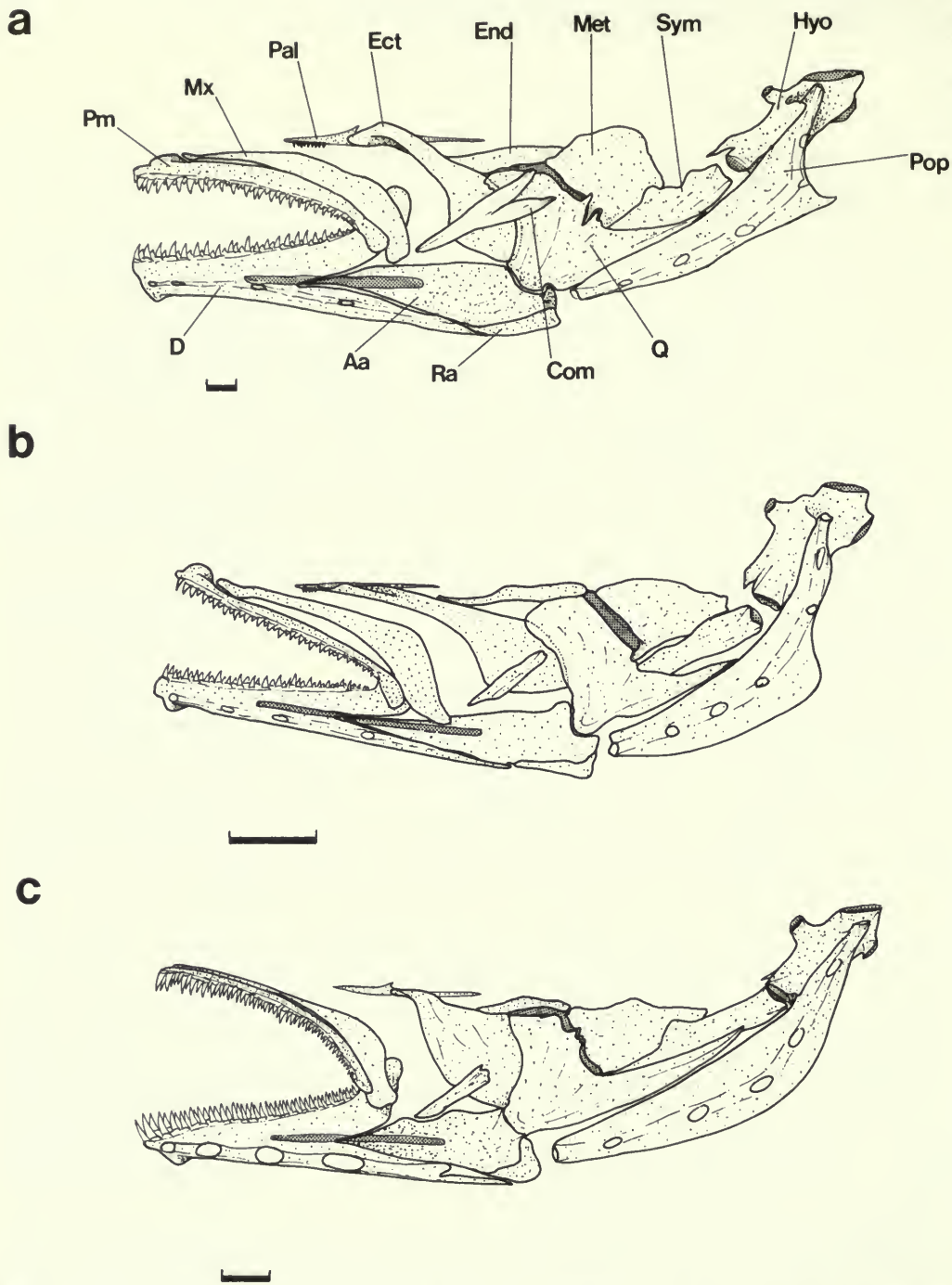


Fig. 43 Hyopalatine arch, preoperculum and jaw bones in (a) *Mastacembelus moorii,* (b) *Mastacembelus ophidium* and (c) *Mastacembelus micropectus;* lateral view, left side.

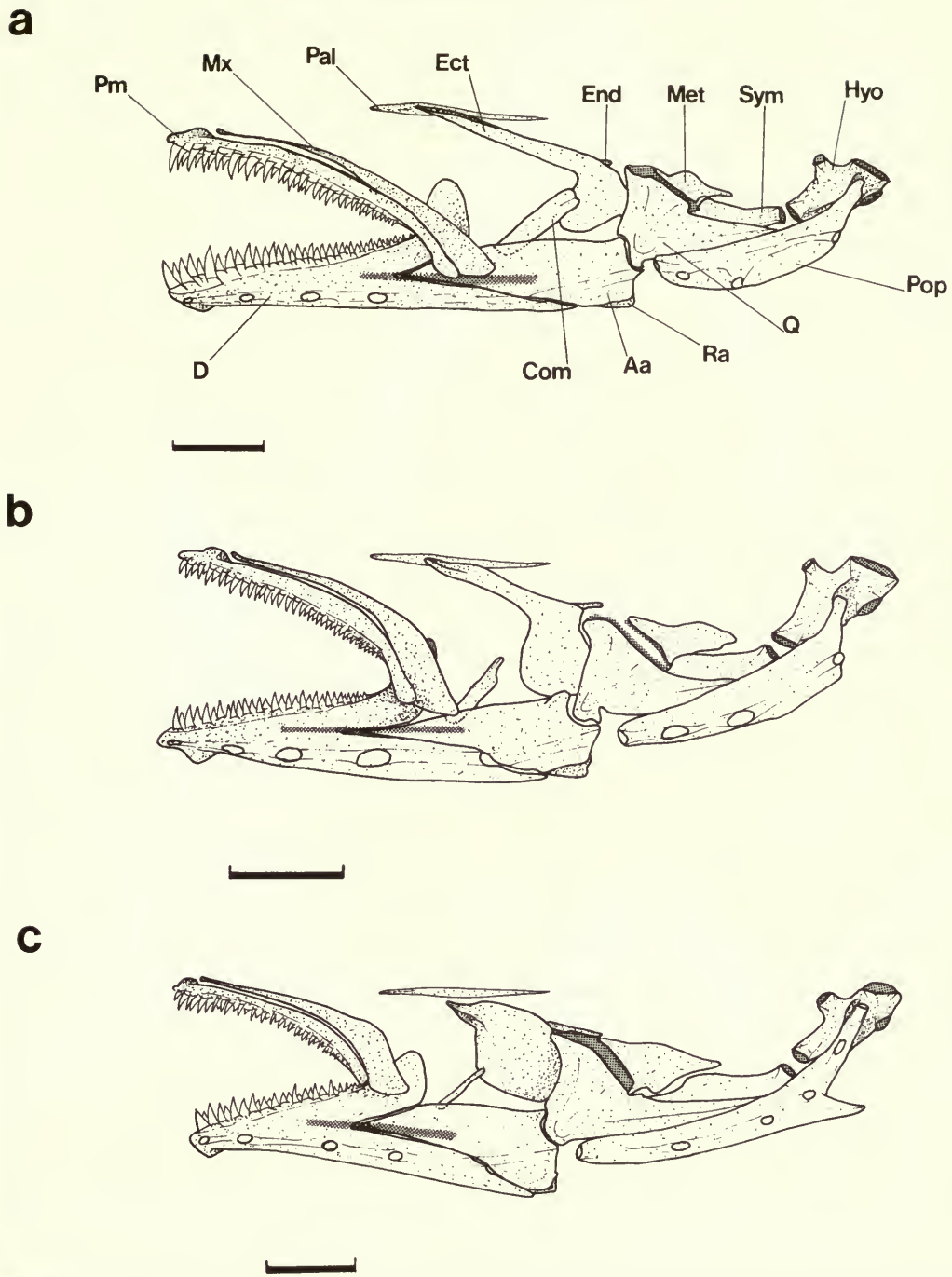


Fig. 44 Hypolatine arch, preoperculum and jaw bones in (a) *Mastacembelus aviceps* (maxilla displaced dorsally), (b) *Mastacembelus crassus,* (c) *Mastacembelus brichardi,* lateral view, left side.

with posteriorly directed tips. The toothed alveolar surface of the premaxillae forms a continuous series with the rostral toothbearing plates.

In the opinion of Roberts (1980: 390) variation in the number of premaxillary rostral plates '... provides perhaps the most important character for distinguishing the species of

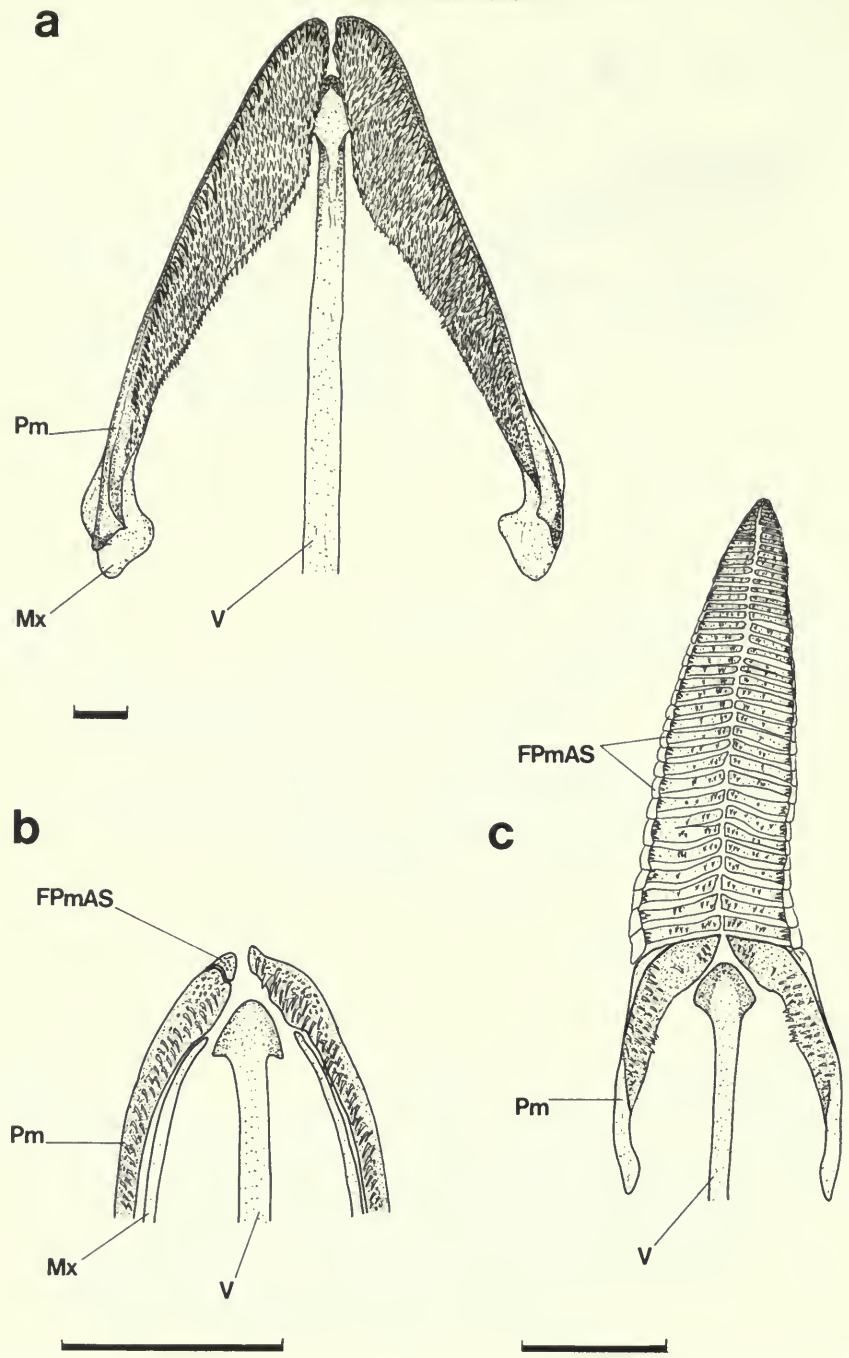


Fig. 45 Upper jaw bones (ventral aspect) in (a) *Mastacembelus cunningtoni,* (b) *Mastacembelus pancalus,* and (c) *Macrognathus aculeatus.*

Macrognathus'. The lowest number occurs in *Macrognathus siamensis* (usually between 9–12 pairs), the highest in *Macrognathus aculeatus* (usually between 38–55 pairs); intermediate between these species are the 14–28 pairs usually found in *Macrognathus aral.* The overall length of the rostral appendage in each of these species is directly proportional to the number of premaxillary plates present.

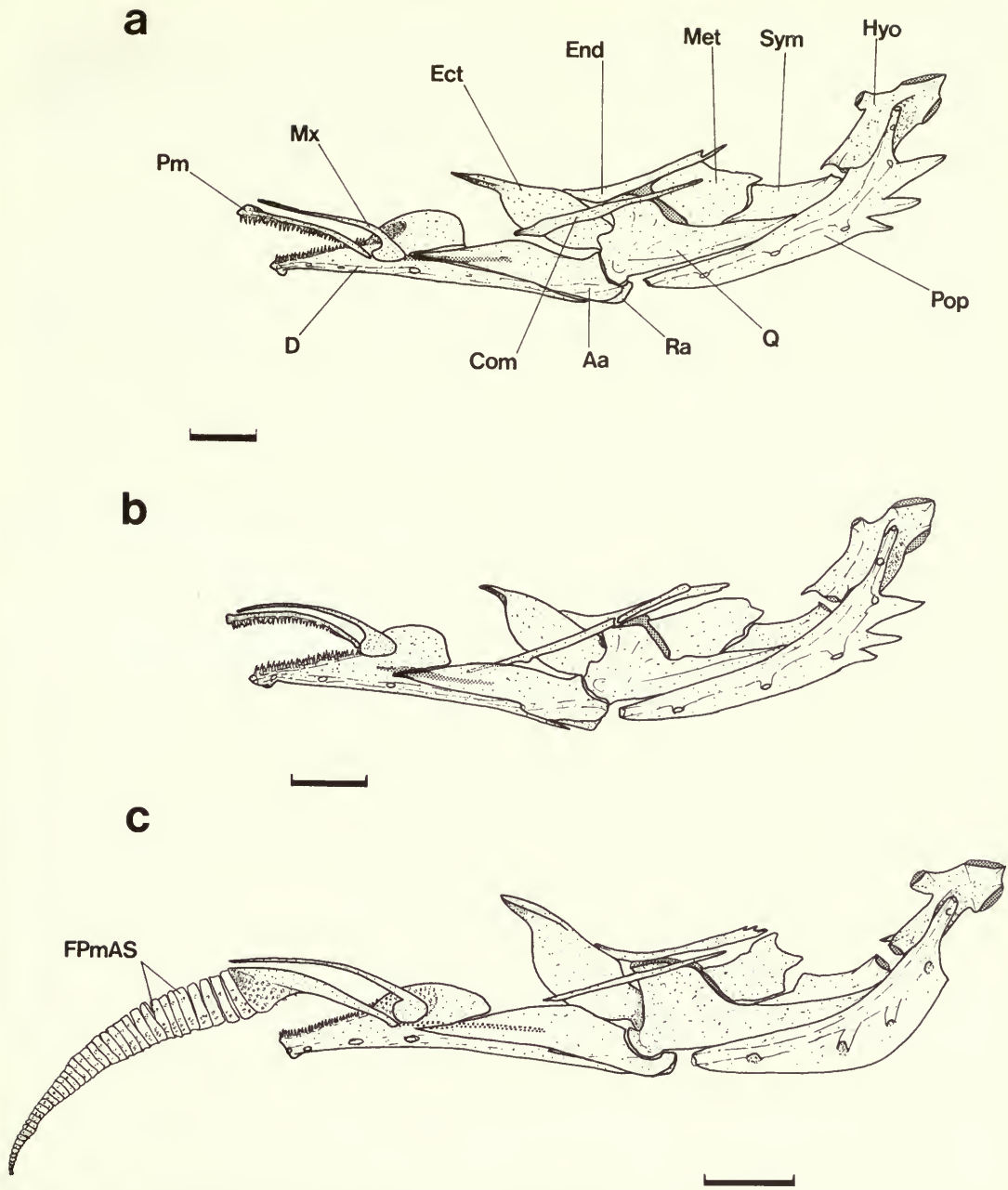


Fig. 46 Hyo-pterygoid arch, preoperculum and jaw bones in (a) *Mastacembelus zebrinus*, (b) *Mastacembelus pancalus* and (c) *Macrognathus aculeatus*; lateral aspect of left side.

Associated with the enlargement and fragmentation of the toothbearing premaxillary alveolar surface in these taxa is the attenuation of the maxilla. In *Mastacembelus zebrinus*, *M. pancalus* and to a greater extent in the *Macrognathus* species, the maxilla has a long, weak anterior process and narrow posteroventral flange (Fig. 46a–c) compared to that of *M. mastacembelus* (Fig. 4) which represents the modal type.

Lower jaw

Interspecific variation in the morphology of the lower jaw is mainly confined to the *dentary* and *coronomeckelian*. The dentary forms almost the entire ventral edge of the mandible in all taxa and in the majority of species its lateral face is pierced by four sensory canal pores. Three pores occur, among the Asian taxa, in *Mastacembelus maculatus, M. pancalus* and in the three *Macrognathus* species; among the African species three pores occur in *Mastacembelus liberiensis, M. greshoffi, M. loennbergii* and *M. ubangensis*.

Dentary pores are reduced to three in *Pillaia* and are absent in *Chaudhuria* (as discussed above p. 36).

The upper or coronoid process of the dentary has two forms, either tall and narrow or low and broad based. The process in *M. mastacembelus* (Fig. 4) is of the tall, narrow type, which also occurs in *Mastacembelus erythrotaenia, M. sinensis, Chaudhuria* and Pillaia among the Asian species examined, as well as in the majority of African species. A low, broad coronoid process occurs in most of the other Asian taxa examined including *Mastacembelus zebrinus, M. pancalus* and the *Macrognathus* species (see Fig. 46a), although the size and shape of the coronoid process in *Mastacembelus armatus* and *M. maculatus* appear to be intermediate between these types.

A low, broad coronoid process also occurs in a number of African species including *Mastacembelus cunningtoni, M. ellipsifer, M. moorii* and *M. platysoma* from Lake Tanganyika, *M. congicus, M. paucispinis* and *M. ubangensis* from Zaire; *M. sclateri* from Sierra Leone, and in *M. goro, M. liberiensis* and *M. niger* from West Africa.

Although the coronoid process in *M. zebrinus, M. pancalus* and the *Macrognathus* species is of a low, broad type similar to that in the African species listed above, it may be distinguished by the posterior expansion of the toothbearing alveolar surface onto its medial face (Fig. 57c). A slight encroachment of the dentary toothplate onto the medial face of the coronoid process was only found in *M. goro* among the African taxa.

The other lower jaw element in which considerable interspecific variation occurs is a sesamoid ossification considered to be the coronomeckelian.

The size and position of the coronomeckelian is a diagnostic feature of all mastacembeloid taxa apart from *Chaudhuria* (Fig. 16a) and *Pillaia* (Fig. 16b). It does not lie dorsal to the anguloarticular in these taxa, but is a small ossicle attached to the posterodorsal edge of Meckel's cartilage, on the medial face of the anguloarticular.

Variation in the overall length of the coronomeckelian is indicated by the position at which its posterior tip lies across the suspensorium. In the Zairean rapids species *Mastacembelus brachyrhinus, M. brichardi, M. crassus* and *M. aviceps* (Fig. 44a–c; and possibly *M. latens*), it is much shorter than the modal condition found, for example, in *M. mastacembelus* (Fig. 4). In species with a tall and narrow coronoid process the coronomeckelian extends dorsocaudally from the dorsomedial margin of the anguloarticular to lie above the anterior face of the ectopterygoid.

Some African taxa have a much larger coronomeckelian in comparison with that of the rapids species described above and *M. mastacembelus*. These include *M. cunningtoni, M. ellipsifer, M. moorii,* and *M. platysoma* from Lake Tanganyika; *M. congicus, M. paucispinis* and *M. ubangensis* from Zaire; *M. sclateri* from Sierra Leone; *M. liberiensis, M. goro* and *M. niger* from West Africa. The coronomeckelian in these species extends well beyond the point occupied by the posterior tip of the bone in *M. mastacembelus*; for example, in *M. cunningtoni* the stout bone extends across the lateral faces of the ectopterygoid and quadrate to the latter's border with the metapterygoid. The coronomeckelian in *M. ellipsifer, M. platysoma* (in which it is barbed) and *M. sclateri* is of approximately equal extent to that in *M. cunningtoni,* while in *M. congicus, M. paucispinis, M. liberiensis, M. goro* (Fig. 50c), *M. niger,* and *M. ubangensis* it is shorter, but only slightly so extending to the posterolateral edge of the ectopterygoid at its border with the quadrate and endopterygoid. The coronomeckelian in *M. moorii* (Fig. 43a) has about the same extent as it does in *M. cunningtoni,* but is distinguished by its prominently forked posterior end.

A feature common to all African species with a long coronomeckelian is the low, broad coronoid dentary process (p. 80). In African species coronomeckelian length is apparently correlated with the type of coronoid process present. Species with a relatively short coronomeckelian (e.g. *M. brichardi* and *M. brachyrhinus*) have, without exception, a tall, narrow coronoid process, whilst those with a relatively long coronomeckelian (e.g. *M. cunningtoni* and *M. liberiensis*) have, again without exception, a low, broad coronoid process. Thus, there is an inverse relationship between coronomeckelian length and coronoid process height.

A low, broad coronoid process occurs (as described above) in *M. zebrinus, M. pancalus* and the *Macrognathus* species. The *Macrognathus* coronomeckelian is a larger bone than that found in *M. mastacembelus*; in *Macrognathus aculeatus* (Fig. 46c) it extends from the dorsomedial margin of the anguloarticular, across the lateral face of the ectopterygoid and quadrate to the latter's border with the metapterygoid.

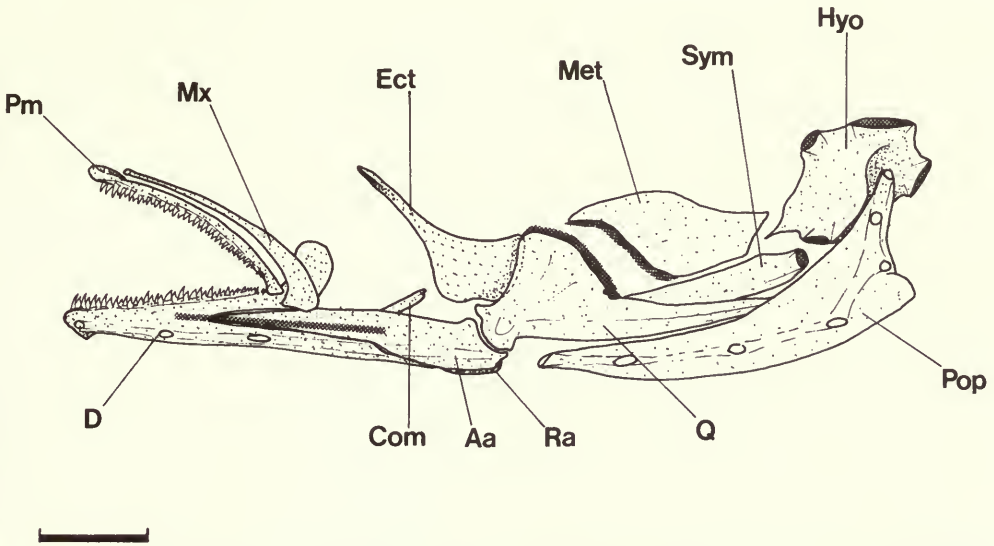


Fig. 47 *Mastacembelus sinensis,* left hyo-pterygoid arch, preoperculum and jaw bones in lateral view.

The length of the coronomeckelian in *M. zebrinus* and *M. pancalus* (which both have a particularly low, broad coronoid process, Fig. 46a & b) also exceeds that in *M. mastacembelus* and even that in *Macrognathus* since it extends posteriorly across the dorsal margin of the anguloarticular to the posterolateral face of the endopterygoid.

A relatively short coronomeckelian occurs in *Mastacembelus sinensis* (Fig. 47) and extends posteriorly from the dorsomedial margin of the anguloarticular but does not reach the anteroventral edge of the ectopterygoid. A relatively tall, narrow coronoid process, described earlier (p. 80) occurs in this species. The type of coronoid process and the condition of the coronomeckelian in Asian mastacembeloids thus appear to have the same relationship as in the African species. The relationship between these bones may be associated with several features of the adductor musculature inserting on them (A_2 & A_3 division); this will be discussed elsewhere (Travers, 1984).

There is little interspecific variation in the morphology of the *anguloarticular*. The lack of an ascending process (coronoid expansion) on the bone in *M. mastacembelus* (Fig. 4) is characteristic of most taxa, but the upper edge of the anguloarticular has a moderately high, broad-based coronoid expansion in *Mastacembelus zebrinus, M. pancalus* and *Macrognathus* species. In these (e.g. see *Macrognathus aculeatus;* Fig. 46c) the dorsal expansion tapers to a low peak which lies just below the anterior end of the coronomeckelian. An

expanded dorsal edge of the anguloarticular is not found in any other Asian or African species. The dorsal edge of the anguloarticular is notched in *Mastacembelus micropectus* (Fig. 43c), the anterior end of the coronomeckelian lying within the notch.

The position of the facet on the anguloarticular (posterodorsal angle) described in *M. mastacembelus* (p. 20) is typical of all taxa apart from the *Macrognathus* species (Fig. 46c) where it notches the dorsal edge anterior to the posterodorsal angle of the bone. Thus, the mandibular joint lies anterior to the posterior end of the anguloarticular.

Hyopalatine arch

The bones of the hyopalatine arch exhibit a number of interspecific differences, but apart from these there are only slight proportional changes in the overall arrangement of the arch.

The anterior edge of the *hyomandibula* shaft in *M. mastacembelus* (Fig. 5) bears a small descending spur. This is an invariable feature of all Asian mastacembeloids with the exception of *Chaudhuria* (Fig. 17a) and *Pillaia* (Fig. 17b), but is not found universally among the African species. For example, among the Tanganyikan species a prominent spur occurs only in *Mastacembelus cunningtoni* and to a lesser extent in *M. micropectus, M. moorii* and *M. ophidium* (Fig. 43 a–c). Other African species with a hyomandibular spur include, *Mastacembelus brachyrhinus, M. marmoratus, M. paucispinis, M. vanderwaali* and the undescribed species.

The hyomandibula and metapterygoid bones are unconnected in the majority of mastacembeloids, a condition typical of almost all species except *Mastacembelus sinensis* (Fig. 47), *Chaudhuria* (Fig. 17a) and *Pillaia* (Fig. 17b). In these taxa the posterolateral edge of the metapterygoid lies in close proximity, attached by connective tissue, to the anteroventral edge of the hyomandibula. The wide gap between these bones in all other mastacembeloids may be related to the particularly large symplectic. Disproportionate growth of this bone, compared to other suspensorial elements, may have resulted in it displacing the metapterygoid and other suspensorial bones away from the hyomandibula (see Figs 43, 44 and 50).

The anterior edge of the *metapterygoid* is connected by a narrow cartilaginous interface to the posterolateral edge of the quadrate in all species examined. The ventral dentate suture, below the cartilage interface, which also connects these elements in *M. mastacembelus* (Fig. 5), is absent in other Asian species and is present in only 4 African species, all from Lake Tanganyika *viz., M. cunningtoni, M. moorii, M. ophidium* and *M. zebratus.*

A small bony spur rises dorsolaterally from the ventral edge of the metapterygoid in *Mastacembelus ubangensis* (Fig. 48). The upper edge of the dorsal lamina on the symplectic in this species is also produced into a short descending process.

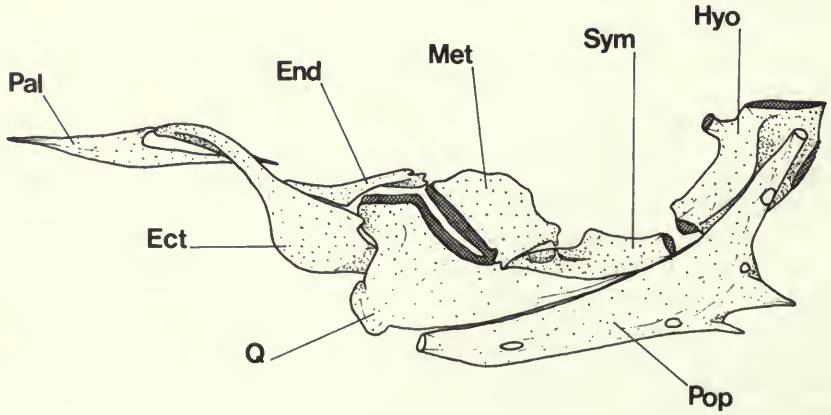


Fig. 48 *Mastacembelus ubangensis,* left hyopalatine arch and preoperculum; lateral aspect.

The *symplectic* (as noted above) is a large element in the hyopalatine arch. Its upper surface, in the majority of species, is produced into a thin lamina with an irregular dorsal edge. Compared with its size in *M. mastacembelus* (Fig. 5), the symplectic is relatively small in *Mastacembelus sinensis* (Fig. 47), *Chaudhuria* (Fig. 17a) and *Pillaia* (Fig. 17b). Associated with its small size in these species is the close contact between the hyomandibula and metapterygoid (discussed above).

The anterior edge of the *quadrate* is indented in *Mastacembelus zebrinus, M. pancalus* and in all *Macrognathus* species (Fig. 46a–c). This curved edge corresponds with the anterior edge of a recess in its anteromedial face, in which lies the large, horn-like ectopterygoid process.

A circular facet on the margin of the quadrate is unique to *Mastacembelus pancalus* (Fig. 46b); the facet articulates with a similar facet on the posterolateral face of the ectopterygoid, dorsal to its horn-like process. Apart from this variation, the form of the quadrate is remarkably constant throughout the group.

Considerable variation occurs in the morphology of the *endopterygoid.* The boomerang-shaped bone in *Mastacembelus mastacembelus* (Fig. 5) also occurs in *M. armatus, M. erythrotaenia, M. oatesii* and *M. unicolor* (see Fig. 49). The anterior process of the endopterygoid in these species extends below and beyond the anterodorsal connection between the ectopterygoid and lateral ethmoid. In no other Asian or African species examined does the endopterygoid contribute to the anterior articulation between the suspensorium (ectopterygoid) and neurocranium (lateral ethmoid). However, in *Mastacembelus maculatus* (Fig. 49c) the anterior tip of the endopterygoid does not lie far from the lateral ethmoid and appears to represent an intermediate condition.

The posterior end of the endopterygoid is distinctly modified in *Macrognathus* (Fig. 46c), *Mastacembelus frenatus* (Fig. 50a), *M. marmoratus, M. niger, M. sclateri* and *M. ubangensis* (Fig. 48). In these taxa the posterior end of the bone is subdivided into 3 prong-like processes whose tips are connected to short tendons running from the *adductor arcus palatini* muscle.

The endopterygoid is less modified in the remaining mastacembeloids examined (e.g. *M. congicus* (Fig. 50b). However, there is a marked tendency for the bone to be reduced in size in three species from the lower Zairean rapids (*Mastacembelus brichardi, M. crassus* and *M. aviceps* Fig. 44a–c: possibly *M. latens* as well). Here the endopterygoid is little more than a small splinter of bone connected to the dorsal end of the quadrate. In *Mastacembelus sinensis, Chaudhuria* and *Pillaia*, however, the bone is entirely absent (see Figs 47 and 17a & b).

The deep anterolateral face of the *ectopterygoid* and its direct articulation with the lateral ethmoid (as described in *M. mastacembelus*, p. 21), are features common to almost all mastacembeloids. The disproportionate anterolateral depth of the ectoptergygoid gives it a sinusoidal shape in most Asian and African taxa. Variation occurs both in the relative depth of the bone in some species, and in the length of its anterodorsal process articulating with the lateral ethmoid.

When compared with other Tanganyikan species, *Mastacembelus moorii* and *M. ophidium* (Fig. 43a & b) have an ectopterygoid with a relatively shallow anterolateral face and a long dorsal process. The bone in Zairean rapids species *M. aviceps* and *M. crassus* (Fig. 44 a & b) is similar to that in *M. moorii* and *M. ophidium.*

The most extreme ectopterygoid variation occurs, however, in *Chaudhuria* (Fig. 17a) and *Pillaia* (Fig. 17b), and to a lesser extent in *Mastacembelus sinensis* (Fig. 47). The bone in *M. sinensis* extends anterodorsally as a long, narrow process, its tip articulating with the lateral ethmoid.

This process is particularly long and anteromedially curved in *Chaudhuria* and *Pillaia;* it does not contact the lateral ethmoid, but extends below it along the lateral face of the vomer.

The depth of the anterolateral face of the ectopterygoid decreases sequentially in *M. sinensis, Chaudhuria* and *Pillaia* (compared Figs 47 and 17a & b), and a progressively smaller region of the bone in these species lies below the quadrate.

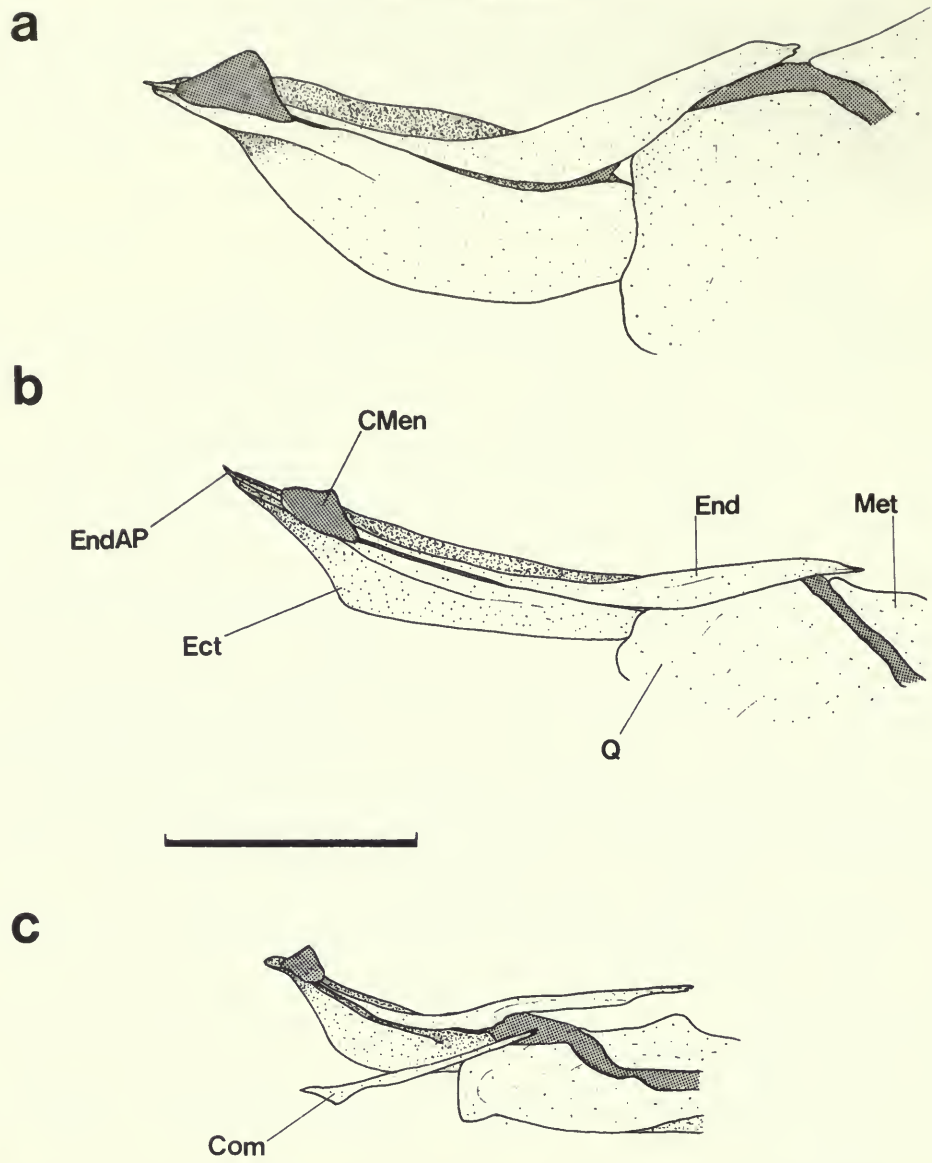


Fig. 49 Endo-ectopterygoid connection, left side, in (a) *Mastacembelus erythrotaenia,* (b) *Mastacembelus armatus* and (c) *Mastacembelus maculatus*; viewed obliquely from a dorso-lateral position.

Modification of the ectopterygoid is associated with the weak, flake-like *palatine* (auto-palatine) in mastacembeloids. The ectopterygoid appears to have replaced the palatine functionally, both with respect to its role as the anterior articulation point of the suspensorium with the neurocranium (discussed in Part II), and with respect to the palatine's contribution to the bony roof of the mouth. The form of the palatine (other than interspecific variation in its dentition and connection to the lateral ethmoid) in *M. mastacembelus* (p. 21 & Fig. 5) is seen in all taxa except *Chaudhuria* and *Pillaia* in which the bone is absent.

All Asian, and the majority of African species lack a palatine, tooth bearing, alveolar surface (dermopalatine). When present, palatine teeth are caniniform with posteriorly directed

tips, arranged in rows, the number of which are interspecifically variable. A single row of teeth occurs in the specimens of *Mastacembelus ophidium* (Fig. 43b) examined, two rows occur in *M. congicus* (Fig. 50b), *M. sclateri, M. loennbergii* and *M. nigromarginatus,* and three rows in *M. longicauda* (Fig. 33a), *M. moorii* (Fig. 43a) and *M. paucispinis* (Fig. 35a

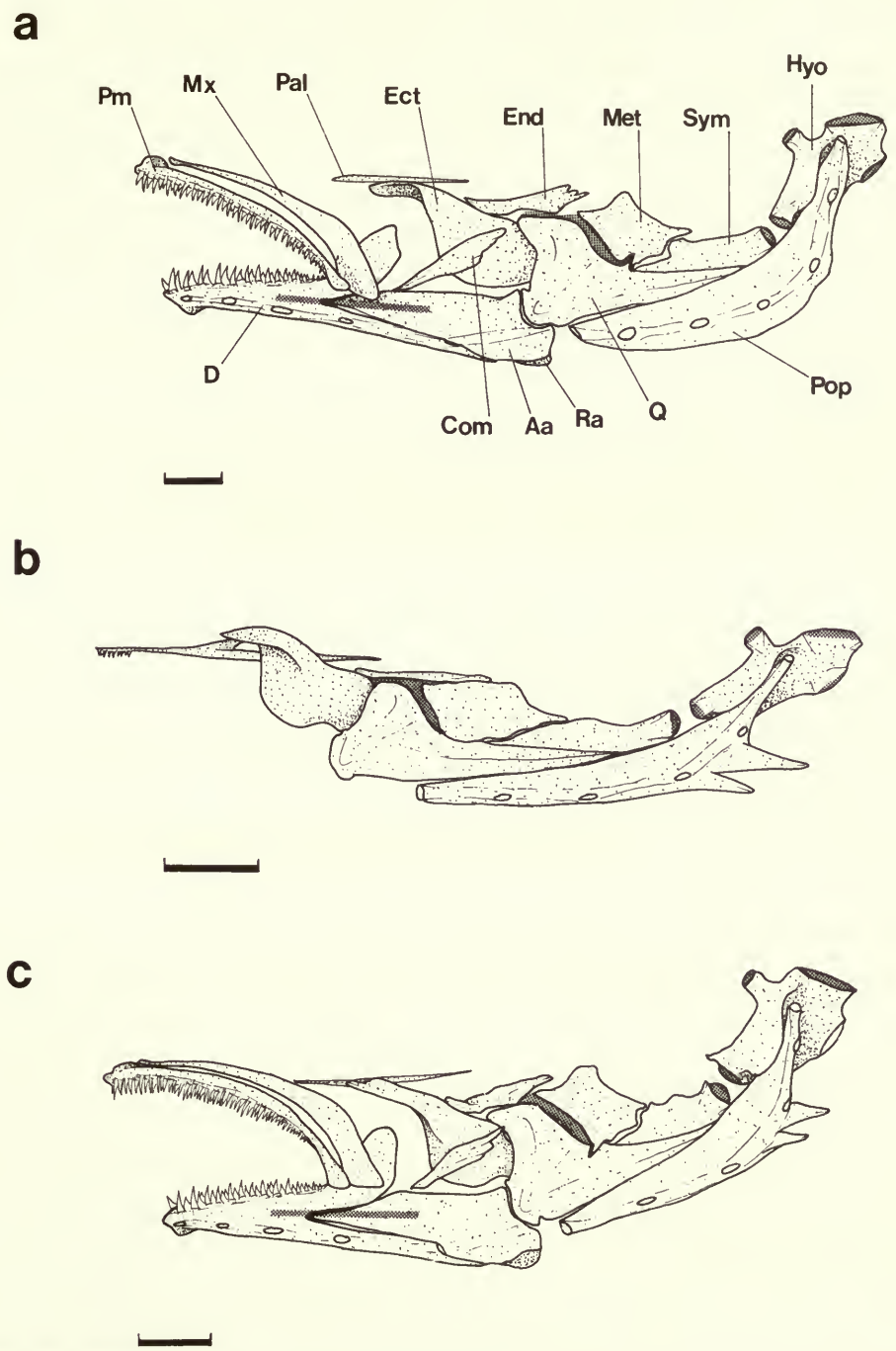


Fig. 50 Left hyopalatine arch, preoperculum and jaw bones in (a) *Mastacembelus frenatus*, (b) *Mastacembelus congicus* (jaw bones not shown) and (c) *Mastacembelus goro*; lateral aspect.

& b). Intraspecific variation in tooth row number is also common; for example a single specimen of *Mastacembelus ellipsifer* has a short toothplate with one row of small caniniform teeth on the left palatine and only a single tooth carried on a very small toothplate, on the right palatine. A specimen of *Mastacembelus vanderwaali* and one of *M. brachyrhinus* have, respectively a single tooth on the left and on the right palatine. Similarly, two teeth are present on the left palatine only of the single specimen of the new *Mastacembelus* species (Fig. 36a & b) from the Cameroonean rapids.

The palatine is connected to the ventrolateral face of the lateral ethmoid in the majority of Asian and in many African species, by a weak, posterodorsally directed spur which ascends from its dorsal edge (see description for *M. mastacembelus,* p. 21). A palatine spur is absent in *Mastacembelus maculatus* (Fig. 26 a & b), *M. pancalus* (Fig. 28 a & b) and the *Macrognathus* species (Figs 29 a & b and 30 a & b) among the Asian mastacembeloids. Among the African species, *Mastacembelus ophidium* (Fig. 43b) is the only East African species lacking a palatine spur, but it is also absent in *Mastacembelus vanderwaali, M. stappersii* and 3 species from the lower Zairean rapids (*M. brichardi, M. aviceps* and *M. crassus;* Fig. 44a–c). Among the West African species a relatively large number, including *Mastacembelus liberiensis, M. goro* (Fig. 50c), *M. longicauda* (Fig. 33a), *M. loennbergii, M. batesii* and *M. brevicauda*, lack the spur.

The palatine spur is thus a relatively constant feature amongst Asian mastacembeloids but has a somewhat mosaic distribution among the African species.

Opercular series

The thinness of the *operculum* (posterior flap), and of the *sub-* and *interopercular* bones are characteristic features of mastacembeloids. Interspecific variation occurs predominantly in the morphology of the *preoperculum*, which shows some intraspecific variability as well. Preopercular features that vary markedly are (1) the number of sensory canal pores, (2) the number of preopercular spines and (3) the relative length of the horizontal limb.

In the Asian and African mastacembeloids the preopercular sensory canal lies within the lateral face of the bone, and opens to the surface *via* a number of circular pores along both the horizontal and vertical limbs.

In most of the Asian species examined there are five sensory canal pores along the ventrolateral face of the bone-enclosed preopercular sensory canal; three on the horizontal limb and two on the vertical limb.

A branched preopercular sensory canal occurs in a number of Asian species. The two posterior pores in the horizontal limb and the ventral pore in the vertical limb of the preoperculum in *Mastacembelus pancalus* and *Macrognathus* species (Fig. 46b & c) lie at the tip of a short descending branch from the main canal. Branched canals are characteristic features of these fishes, associated with the broad, lateral face and relatively short length of the preoperculum. Only two short branches descend from the main canal in *Macrognathus aculeatus* (Fig. 46c) which has a particularly short preoperculum.

The preopercular bones in *Chaudhuria* and *Pillaia* are exceptional amongst mastacembeloids. In *Pillaia* (Fig. 18b) the canal is indistinct and is restricted to the central region of the lateral face of the bone, whereas in *Chaudhuria* (Fig. 18a) there is no canal in the preoperculum.

Based on the number of preopercular canal pores, the African taxa can be divided into two groups *viz.,* those with 5 and those with 4 pores; all the Asian taxa have 5 pores. The African species with 5 pores include half the species found in Lake Tanganyika (*Mastacembelus albomaculatus, M. ellipsifer, M. frenatus, M. moorii, M. ophidium* and *M. platysoma*), as well as *Mastacembelus shiranus, M. stappersii, M. paucispinis, M. reticulatus* and the undescribed species. Almost all the remaining African species have 4 pores, the only exception being 3 species from the lower Zairean rapids, of which *Mastacembelus brachyrhinus,* has 3 and *M. crassus* and *M. aviceps* have 2 pores.

A clearly reductional sequence is manifest in the endemic Zairean rapids species, running from 5 pores in *M. paucispinis*, through 4 in *M. brichardi*, 3 in *M. brachyrhinus*, to 2 pores in the highly derived *M. crassus* and *M. aviceps*. Furthermore, in *M. crassus* and *M. aviceps* the dorsal opening of the preopercular sensory canal does not lie at the tip of the bone but along its posterolateral edge (Fig. 44a & b).

The lack of spines on the preoperculum in *M. mastacembelus* (p. 23) is a feature common to a number of Asian species including *Mastacembelus maculatus*, all *Macrognathus* species, *Mastacembelus sinensis*, *Chaudhuria* and *Pillaia*.

Preopercular spines occur in the other Asian species examined namely *Mastacembelus armatus*, *M. erythrotaenia*, *M. oatesii*, *M. unicolor*, *M. zebrinus* and *M. pancalus*. Although intraspecific variability in the number of spines is common, generally three or four occur in each of these species. This variability may even occur between the number of spines on the left and right preoperculum in the same individual. For example, in a specimen of *M. zebrinus* (Fig. 46a) three spines are present on the left and four on the right side. Considerable variation in preopercular spines also occurs amongst the African mastacembeloids. Many species from east and southern Africa have a single spine, e.g. *Mastacembelus albomaculatus*, *M. moorii*, *M. plagiostomus*, *M. platysoma*, *M. tanganicae* and *M. zebratus*. However, *Mastacembelus cunningtoni* and *M. ellipsifer* are characterised by two spines, while *M. frenatus*, *M. ophidium*, *M. micropectus*, *M. shiranus*, *M. stappersii* and *M. vanderwaali* lack preopercular spines. Spines are absent in the west African *Mastacembelus niger*; a single spine occurs on the left side in one specimen of *M. batesii* and *M. nigromarginatus*. The remaining west African species have two or three spines, as do *Mastacembelus ubangensis* and the undescribed species.

Among the mastacembeloids endemic to the Zairean rapids (Roberts & Stewart, 1976) there appears to be a sequential loss of spines from two in *Mastacembelus paucispinis*, one in *M. brichardi* and *M. brachyrhinus*, to none in the highly derived *Mastacembelus crassus* and *M. aviceps*. Apart from these rapid-dwelling species the number of preopercular spines varying from none to four, appears to have a mosaic distribution among both the Asian and the African mastacembeloid taxa.

The dimensions of the horizontal preopercular limb vary from relatively short and wide (e.g. *Mastacembelus ophidium* and *M. micropectus*, Fig. 43b & c) to long and narrow (e.g. *Mastacembelus vanderwaali* and *M. cunningtoni*) among members of both the Asian and the African mastacembeloids. This variation may be associated with the neurocranial and jaw length.

The vertical limb is generally shorter than the horizontal limb in the majority of mastacembeloids. However, the vertical limb is particularly long in four species from west Africa; *Mastacembelus longicauda*, *M. brevicauda*, *M. nigromarginatus* and *M. reticulatus*.

Hyoid arch

There is remarkably little interspecific variability in the morphology of the hyoid arch. The condition of the arch in *Mastacembelus mastacembelus* (p. 23) is typical of that found generally among both Asian and African members of the suborder.

Variation in the relative length of the *basihyal*, as compared with its condition in *M. mastacembelus* (Fig. 8), occurs in some species. It is relatively short in *Mastacembelus moorii* and *Mastacembelus ophidium* from Lake Tanganyika, having a wide dorsal surface and deep ventral ridge, the former feature giving the bone in *M. moorii* a particularly wide, spatulate surface. The long basihyal in *Mastacembelus erythrotaenia* is distinguished by its relatively narrow dorsal surface and low ventral ridge.

The *anterior* and *posterior ceratohyal* are joined by a series of dentate sutures in all mastacembeloids except *Chaudhuria* (Fig. 20ai) and *Pillaia* (Fig. 20bi). In these taxa a distal flange on the anterior ceratohyal lies in a recess on the posterior face of the posterior ceratohyal; the two elements are connected by a straight suture and a cartilaginous interface.

A variable number of irregular short spikes extend into the cartilaginous interface between

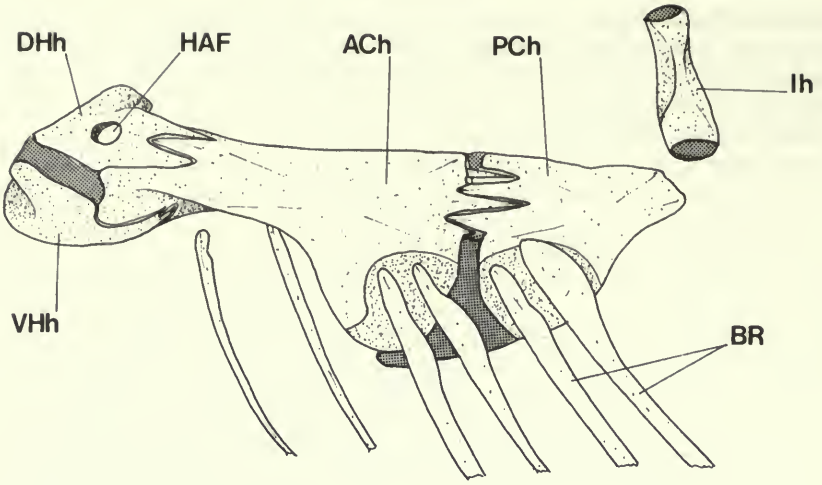


Fig. 51 *Mastacembelus sinensis*, left hyoid arch, in lateral view.

the bones in *Mastacembelus sinensis* (Fig. 51) seemingly a variant of the condition shown by the majority of species.

The *urohyal* shows considerable variation (compared to its condition described in *M. mastacembelus* p. 24), particularly with respect to its length and the arrangement of its posterior, prong-like processes. However, it is in its connection with basibranchial 1 that the most prominent interspecific variation occurs.

A direct connection between the urohyal and basibranchial 1, either by way of an ascending process (or processes) or a synchondral joint (discussed below) occurs in all Asian mastacembeloids except *Mastacembelus sinensis, Chaudhuria* and *Pillaia.* In *M. sinensis* (Fig. 52a) and *Pillaia* the tip of an ascending process on the dorsal surface of the urohyal is connected to the underside of basibranchial 2. In *Chaudhuria* there is neither an ascending urohyal process nor a direct articulation with basibranchial 1.

Since none of the African species has a direct connection between the anterodorsal surface of the urohyal and the ventral edge of basibranchial 1, the process on the urohyal and its connection to basibranchial 1 in the Asian mastacembeloids appears to have resulted in a variety of specific characters.

The urohyal in *Mastacembelus zebrinus* (Fig. 52b) is connected more closely to basibranchial 1 and may represent an intermediate condition between the type of urohyal development seen in *M. mastacembelus* and the direct urohyal–basibranchial 1 articulation in the *Macrognathus* species. The anterodorsal surface of the urohyal in *M. zebrinus* lies directly below the ventral edge of the keel on basibranchial 1 (p. 90). A long, narrow process ascends anterodorsally from the urohyal along the posterior edge of the keel on basibranchial 1. The anterior edge of this process is connected to the posterior edge of the keel, and its tip contacts the ventral surface of basibranchial 2.

Although the urohyal lacks an ascending process in a number of Asian mastacembeloids, these taxa are distinguished by a direct articulation between the anterodorsal surface of the urohyal and the keel on basibranchial 1.

In place of an ascending process in *Mastacembelus pancalus* (Fig. 53a) there is a depression with wide lateral and posterior rims. The ventral edge of basibranchial 1 is cartilaginous and articulates synchondrally with the dorsal surface of this depression in the urohyal.

In *Macrognathus siamensis* (Fig. 53b) the dorsal surface of the urohyal is level but has

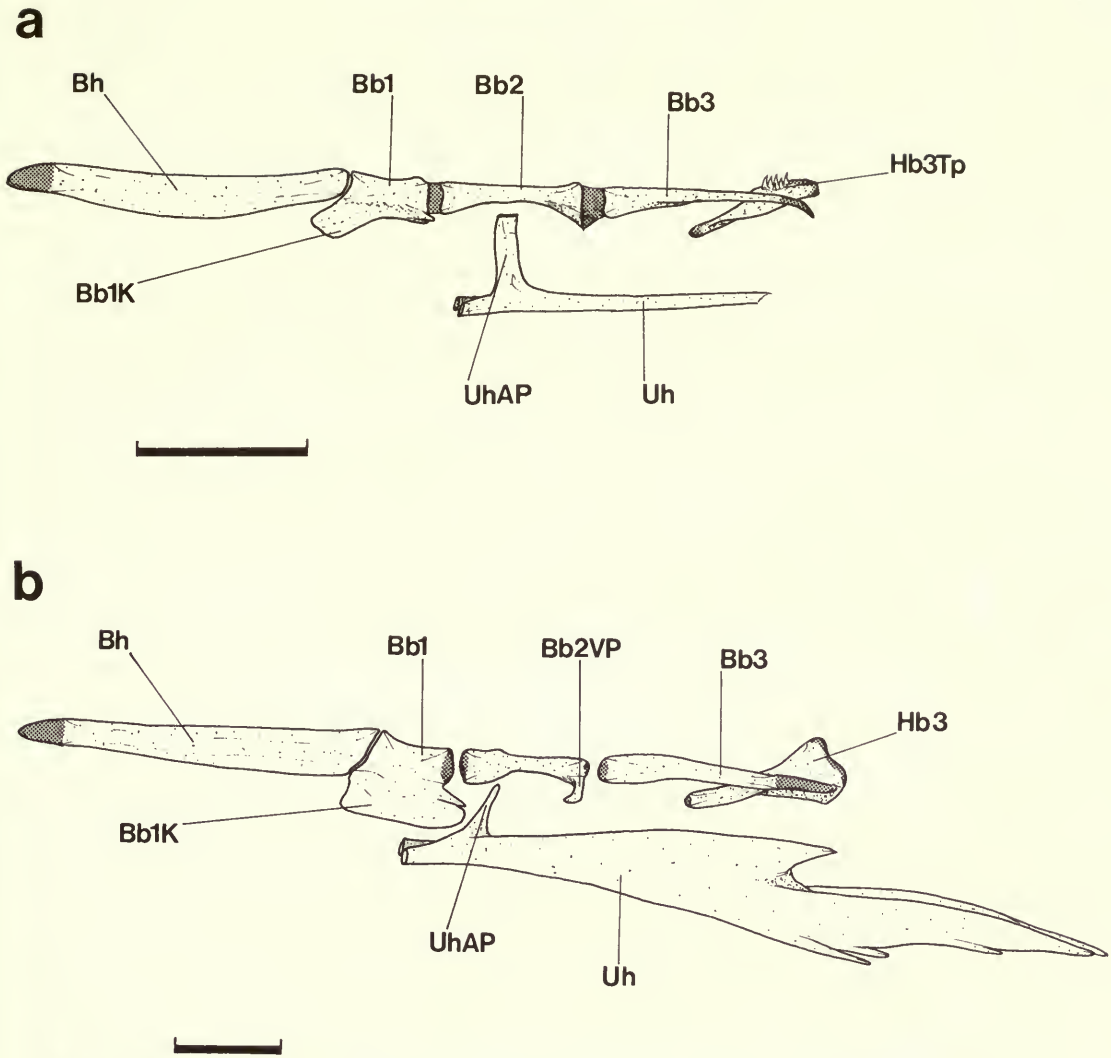


Fig. 52 Basibranchial/urohyal arrangement in (a) *Mastacembelus sinensis* and (b) *Mastacembelus zebrinus*; lateral aspect, left side.

a shallow groove in which the cartilaginous ventral edge of basibranchial 1 articulates. The bifurcated anterior end of the urohyal in *Macrognathus aral* and *Macrognathus aculeatus* (Fig. 53c) forms a shallow longitudinal groove along its dorsal surface in which lies the cartilaginous ventral edge of basibranchial 1. The posterior region of the urohyal in *Mastacembelus pancalus* and the *Macrognathus* species (Fig. 53a–c), generally lacks the prong-like processes that occur in other mastacembeloid taxa. The urohyal in *Mastacembelus oatesii* (Fig. 54) also lacks an ascending process. The anterior tips of the urohyal in this species are particularly deep and form a groove between their medial edges. The ventral edge of basibranchial 1 lies along this groove but it is not cartilaginous, and the elements do not articulate in the manner described for *M. pancalus* and *Macrognathus.* An ascending process (or processes) on the dorsal surface of the urohyal in *Mastacembelus armatus, M. erythrotaenia* and *M. maculatus* is connected to the ventral edge of basibranchial I in an arrangement similar to that in *M. mastacembelus* (p. 24, Fig. 9).

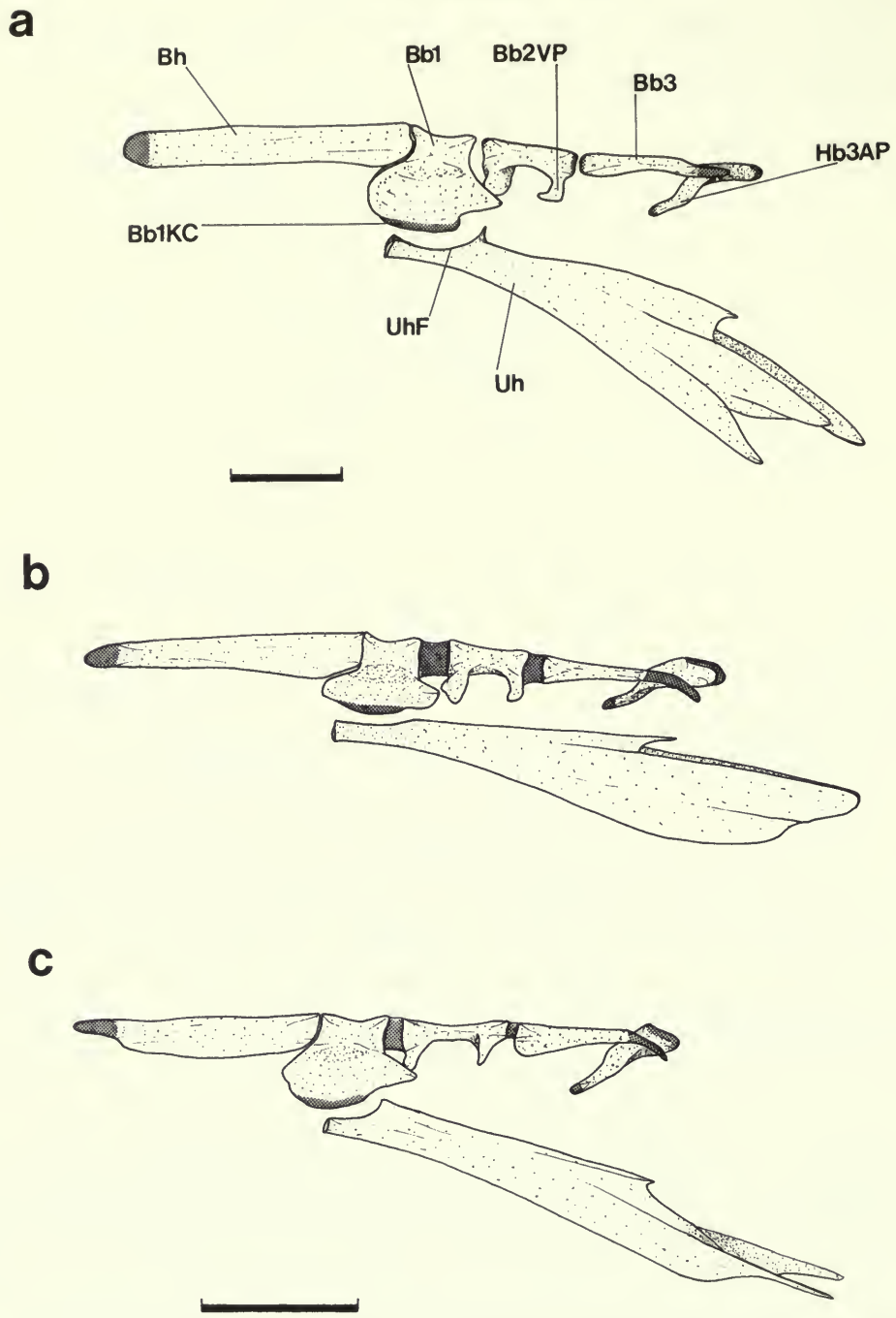


Fig. 53 Basibranchial/urohyal arrangement in (a) *Mastacembelus pancalus,* (b) *Macrognathus siamensis* and (c) *Macrognathus aculeatus*; lateral aspect, left side.

Branchial arches

The basibranchial elements described in *M. mastacembelus* (Fig. 8) are typical of those found throughout the group. The deep ventral 'keel' on *basibranchial 1* is a constant feature of almost all mastacembeloid taxa, but is absent in *Mastacembelus sinensis, Chaudhuria* and

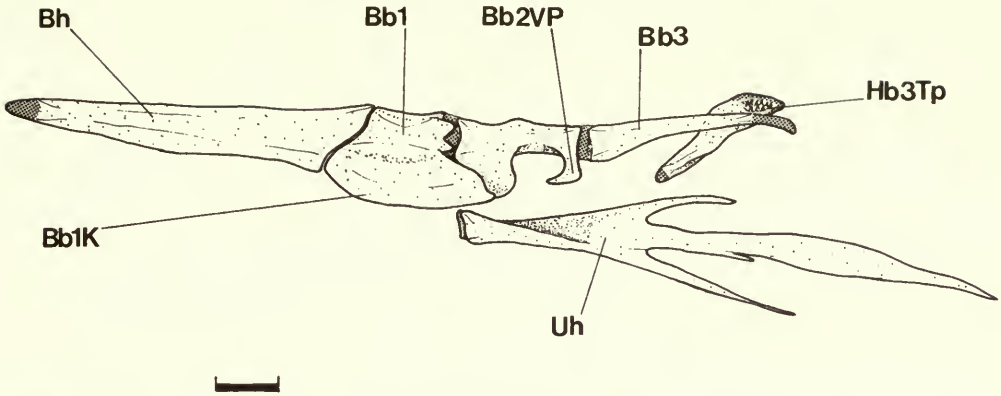


Fig. 54 *Mastacembelus oatesii,* basibranchial/urohyal arrangement; lateral aspect, left side.

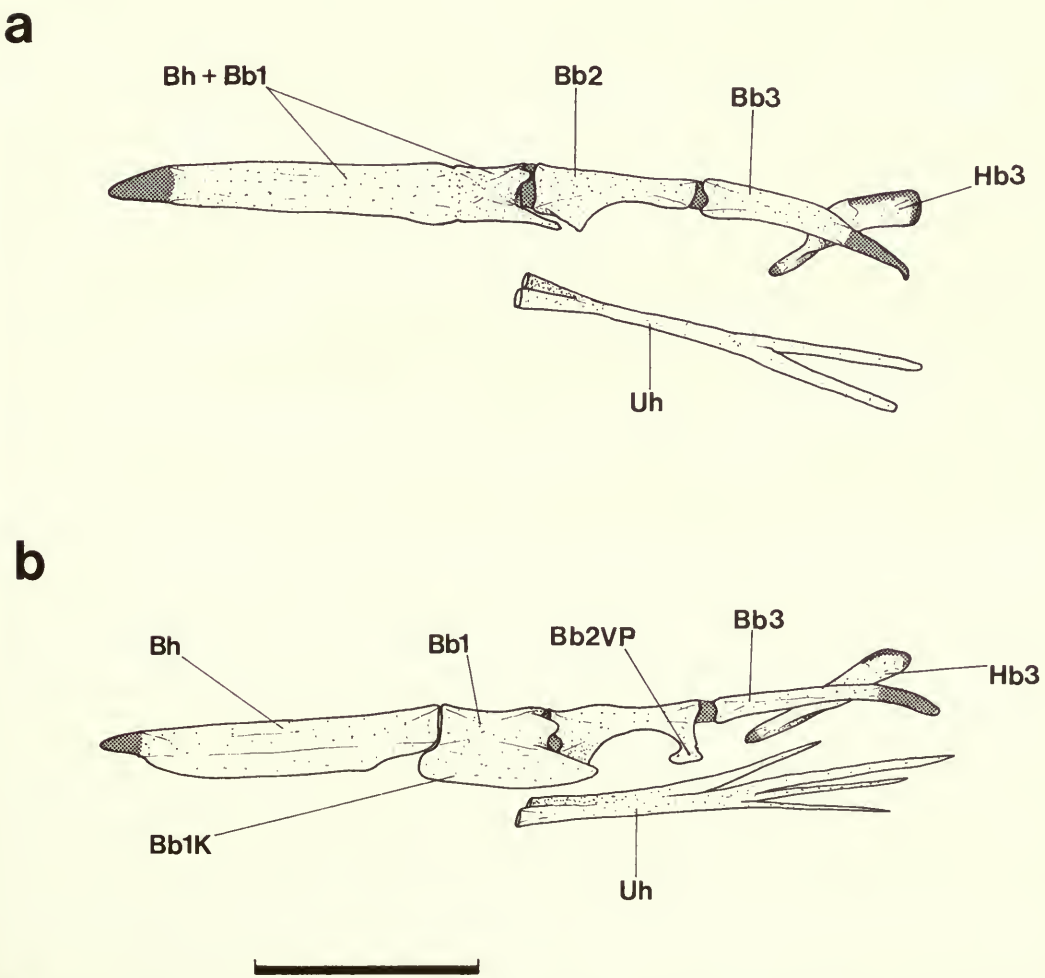


Fig. 55 Basibranchial/urohyal arrangement in (a) *Mastacembelus aviceps* and (b) *Mastacembelus crassus*; lateral aspect, left side.

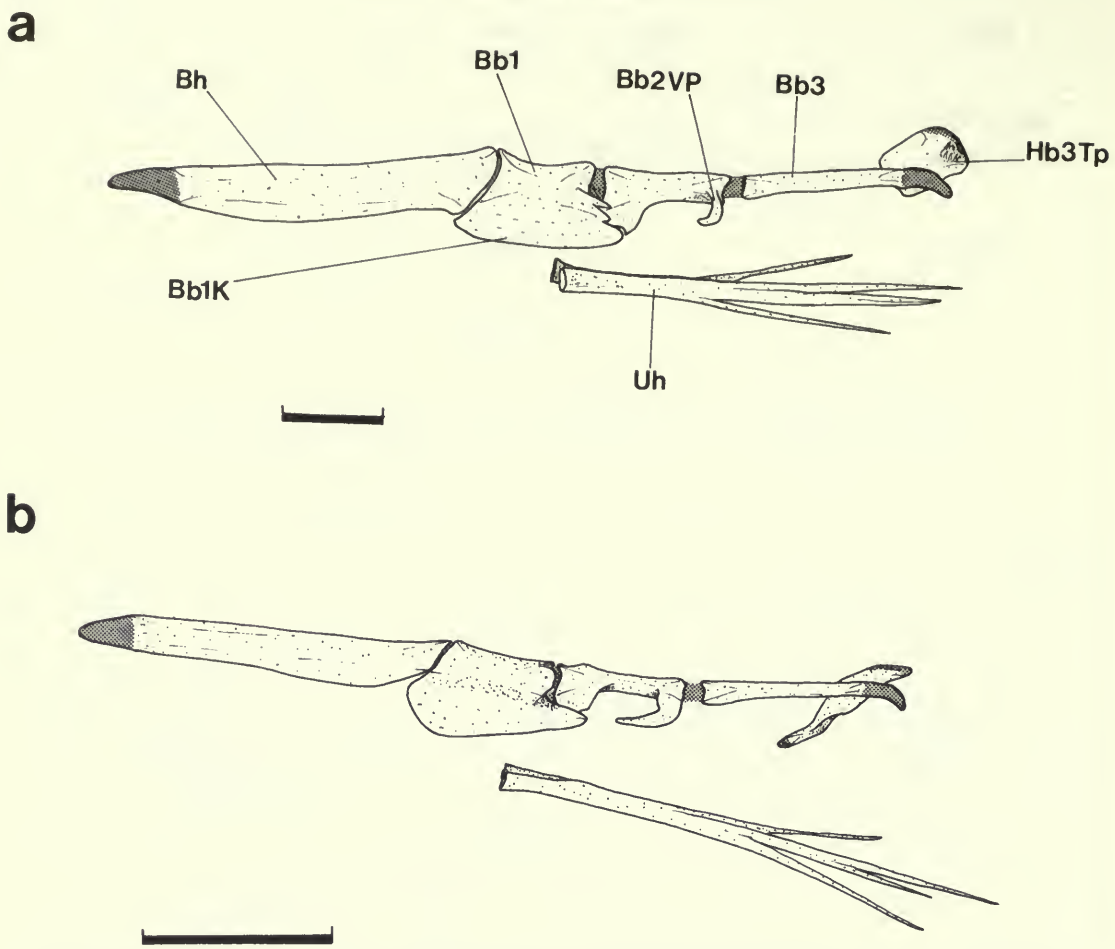


Fig. 56 Basibranchial/urohyal arrangement in (a) *Mastacembelus nigromarginatus* and (b) *Mastacembelus ubangensis*; lateral aspect, left side.

Pillaia (see p. 46). The keel is particularly well-developed in *Mastacembelus pancalus* and *Macrognathus* species (Fig. 53a–c) where the ventral knife-edge is cartilaginous.

The only variation in the 'keel' on basibranchial 1 among the African species is seen in the relatively low 'keel' of *Mastacembelus aviceps* and *M. crassus* (Fig. 55a & b).

A pair of processes, each descending from the posterolateral corner of *basibranchial 2* (as described in *M. mastacembelus* p. 25, Fig. 9), occur in most mastacembeloids. *Mastacembelus sinensis, Chaudhuria* and *Pillaia* among the Asian, and *M. aviceps* among the African species are again exceptional in that they lack these processes.

The tips of the descending processes on basibranchial 2 are connected ligamentously to the posteroventral edge of the keel on basibranchial 1. Part ossification of the ligaments occurs in two African species, *Mastacembelus nigromarginatus* and *Mastacembelus ubangensis* (Fig. 56a & b). Among the west African species each ligament is almost completely replaced by the descending processes arching longitudinally across the ventral surface of basibranchial 2. The anterior tips of the processes in these species contact the keel on basibranchial 1, and a pair of ventral arches of this type are a characteristic feature of *Mastacembelus goro, M. flavomarginatus, M. greshoffi, M. longicauda, M. loennbergii, M. batesii* and *M. brevicauda* (e.g. Fig. 57a–c). The ventral aorta passes longitudinally along the surface of the basibranchial elements and lies between the descending arches on basibranchial 2.

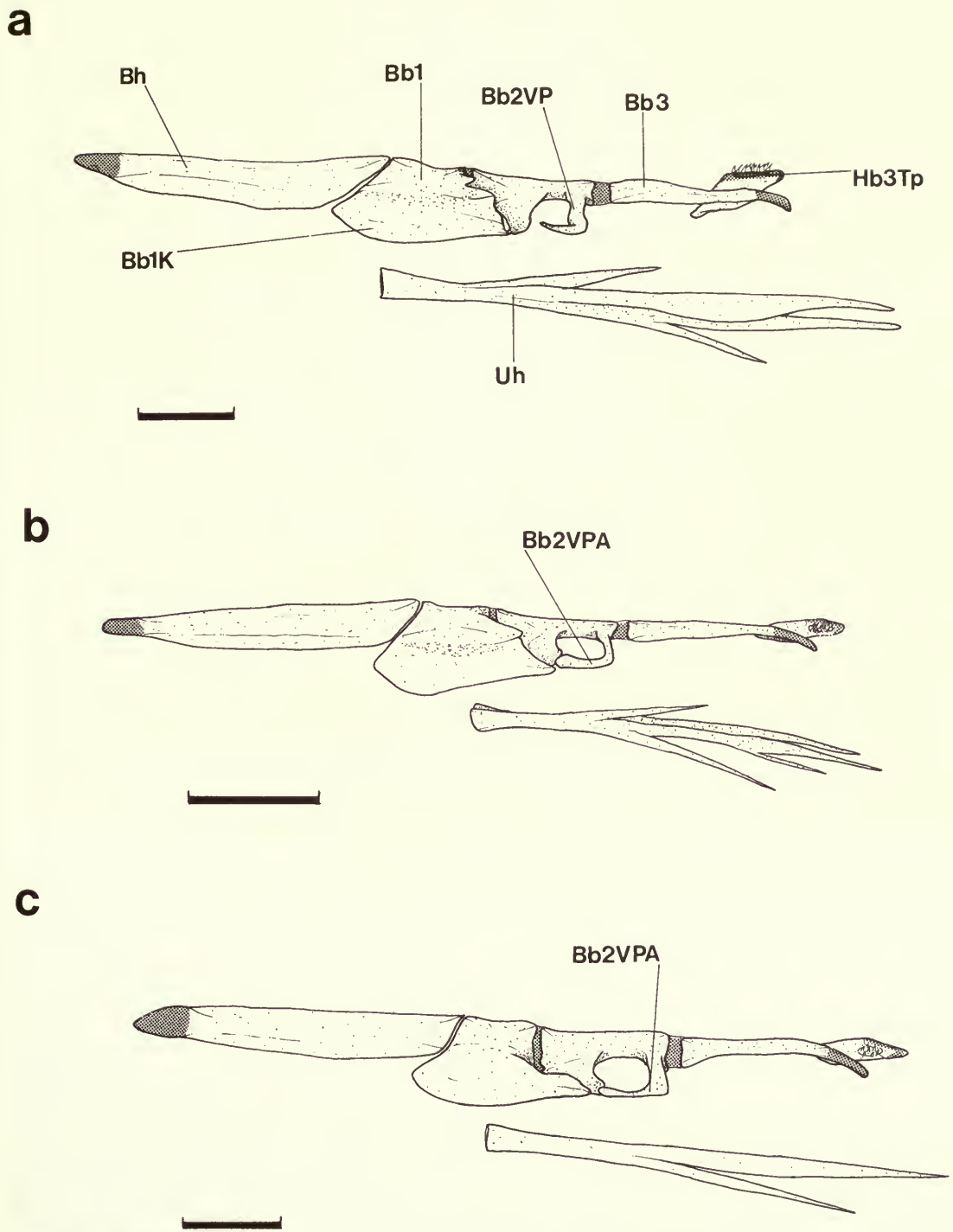


Fig. 57 Basibranchial/urohyal arrangement in (a) *Mastacembelus longicauda,* (b) *Mastacembelus loennbergii* and (c) *Mastacembelus batesii*; lateral aspect, left side.

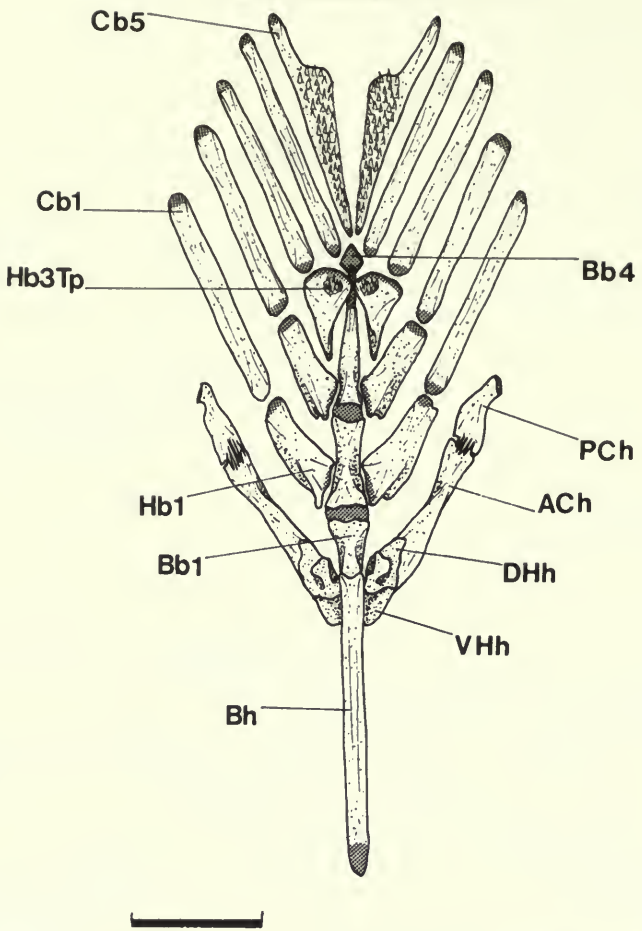


Fig. 58 *Mastacembelus maculatus,* hyoid and lower gill arches in dorsal view.

The first afferent arteries pass between each arch and the ventral surface of basibranchial 2.

There is only slight interspecific variation in the hypobranchial bones, apart from two features of *hypobranchial 3;* the presence of a small toothplate joined to the dorsal surface, and the lack of an anteroventral process extending below hypobranchial 2.

A round toothplate fused to the dorsal surface of hypobranchial 3 (Fig. 58) occurs in the Asian mastacembeloids except *M. mastacembelus* (Fig. 8) and *Pillaia* (Fig. 20bi).

A fused toothplate on hypobranchial 3 is also of frequent occurrence among the African taxa (e.g. Figs 60–63). It is, however, absent in the endemic species from the lower Zairean rapids (i.e. *Mastacembelus paucispinis, M. brachyrhinus, M. brichardi, M. crassus, M. aviceps*), and *Mastacembelus marmoratus, M. niger, M. sclateri, M. ubangensis* and the undescribed species.

The second important feature of hypobranchial 3 is its long anteroventral process. In *M. mastacembelus* this process extends anteriorly below hypobranchial 2 (Fig. 8), with its tip connected ligamentously to basibranchial 2. This process occurs universally among the Asian taxa (e.g. Figs 58 & 59) and in the majority of African species (e.g. Figs 60 & 61). It is absent in a number of species from western Africa, including *Mastacembelus batesii, M. brevicauda, M. flavomarginatus, M. goro, M. greshoffi, M. liberiensis, M. loennbergii, M. longicauda, M. niger, M. nigromarginatus, M. reticulatus* and *M. sclateri* (see Figs 56, 57 & 62). In these species if the anterior edge of hypobranchial 3 is produced at all it is

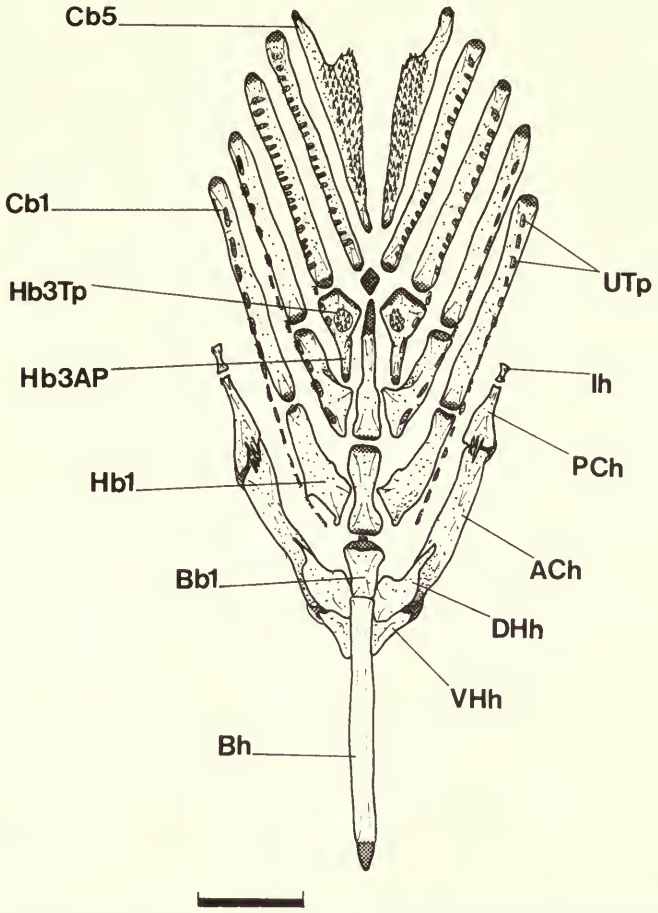


Fig. 59 *Mastacembelus zebrinus,* hyoid and lower gill arches in dorsal view.

in the form of a short stump, (e.g. *M. liberiensis,* Fig. 63); but there is no ligamentous attachment to basibranchial 2.

Ceratobranchial 5 is the only other ventral gill arch element to which a toothplate is fused. Interspecific variation in the dorsal surface area of the toothplate is related to its degree of medial expansion. Compared with *M. mastacembelus* (Fig. 8), it is particularly narrow in *M. maculatus* (Fig. 58), whereas, the Tanganyikan species *Mastacembelus cunningtoni* and *M. tanganicae* (Figs 60 & 61) are distinguished by their wide medial expansion of the toothplate. The toothplate does not contact its partner in the midline in any species.

The dentition of the toothplates fused to the ventral gill arch elements consist of caniniform teeth, tips directed posteriorly, varying interspecifically in size. The small, unfused toothplates irregularly positioned along the length of ceratobranchials 1–4 and hypobranchials 1–3, show considerable inter and intra-specific variation in size and number. When present, the dentition is of small conical teeth (see Figs 59–61).

The dorsal gill arch elements in all taxa lie posterior to the neurocranium, and show a remarkable lack of interspecific variability. The arrangement of the *epibranchial (1–4)* and *pharyngobranchial (2–3)* bones in *M. mastacembelus* (Fig. 10a & b, p. 26) is typical for most mastacembeloids.

Pharyngobranchial 1 is lacking in all mastacembeloids. This may be associated with the posterior position of the dorsal gill arch elements since its absence is a feature common to most eel-shaped fishes (Nelson, 1970). In one specimen of *Pillaia,* pharyngobranchial 2 is

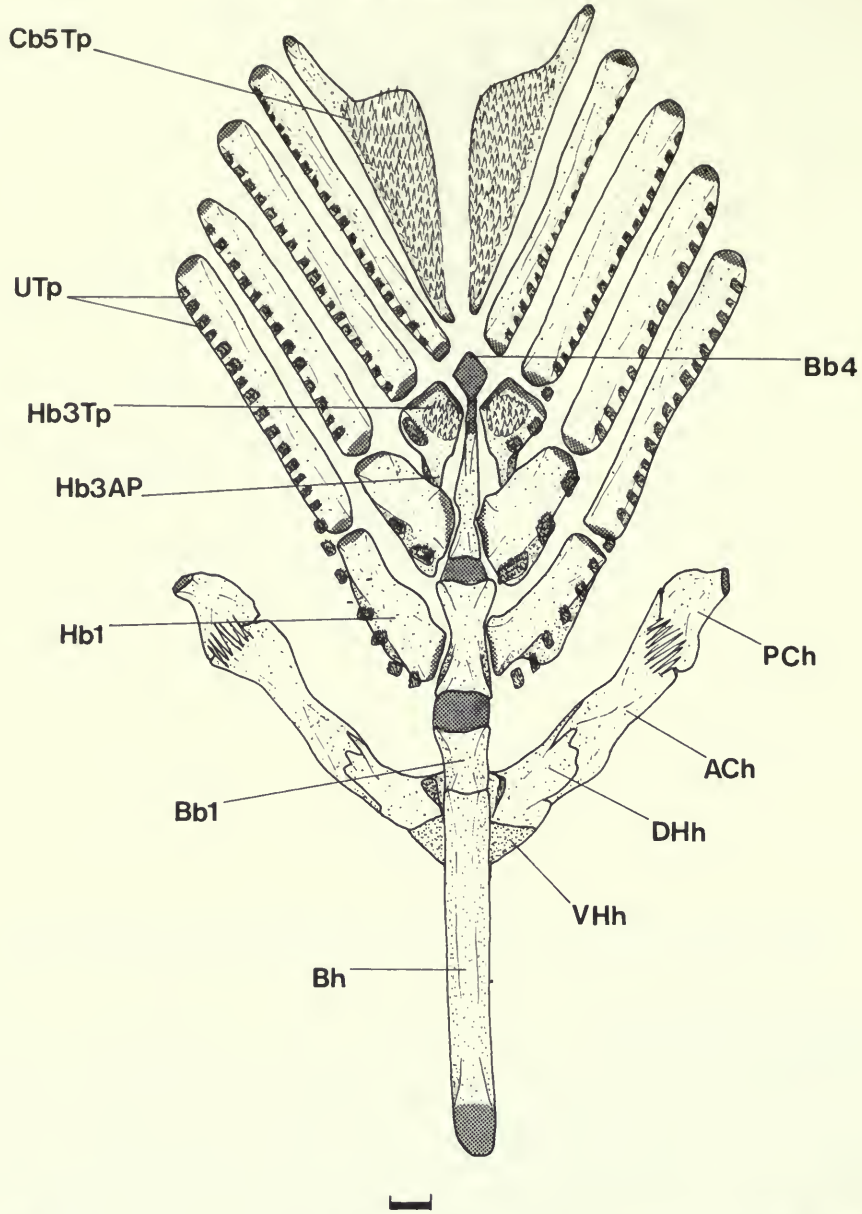


Fig. 60 *Mastacembelus cunningtoni,* hyoid and lower gill arches in dorsal view.

present as a small cartilaginous element within a collagenous strand linking the tips of epibranchials 1 and 2, (a condition generally found only at an early embryonic stage), but in a second specimen a well-developed pharyngobranchial 2 is present (Fig. 20bii).

The anteromedial extension of pharyngobranchial 3, (beyond its point of contact to epibranchial 2) and its connection to the tip of both pharyngobranchial 2 and epibranchial 1, is a feature common to most taxa (as seen in *M. mastacembelus,* Fig. 10a & b). However, pharyngobranchial 3 lacks an anterior extension in *Chaudhuria* (Fig. 20aii) and *Pillaia* (Fig. 20bii); the arrangement of this bone in *M. sinensis* (Fig. 66) appears to be somewhat intermediate between that found in *Chaudhuria* and *Pillaia* and the modal condition. The fourth pharyngobranchial element is invariably cartilaginous in mastacembeloids.

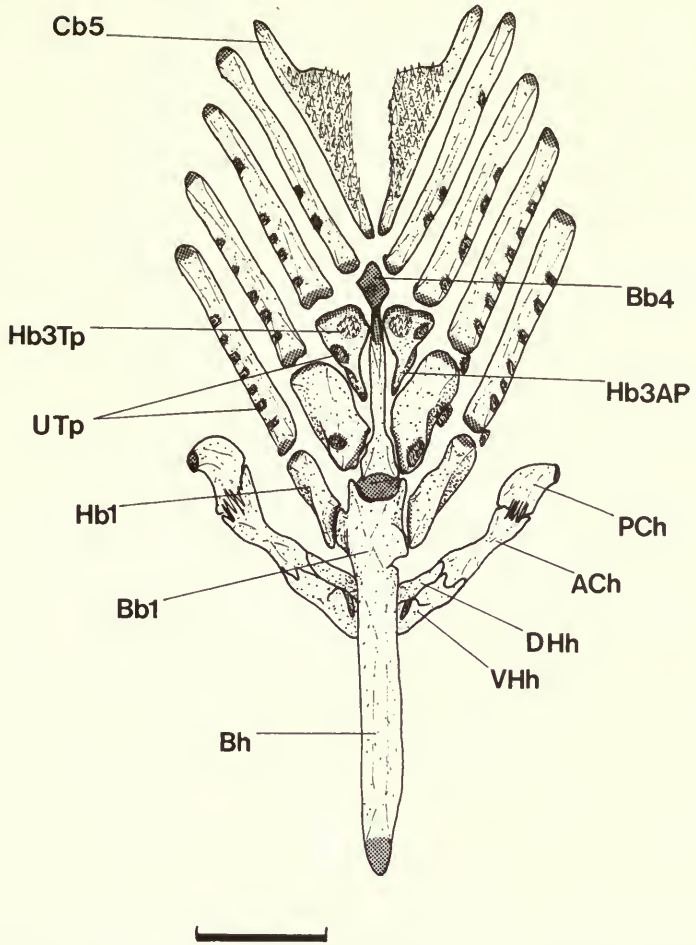


Fig. 61 *Mastacembelus tanganicae,* hyoid and lower gill arches in dorsal view.

The most variable feature of the dorsal gill arch elements is the *unfused toothplates.* Except in *Chaudhuria* and *Pillaia,* small irregularly positioned toothplates lie along the anteroventral face of epibranchials 1 and 2 in all Asian mastacembeloids (Fig. 10a). Amongst the African representatives, Lake Tanganyikan species have similar epibranchial toothplates, (discussed below), but apart from these groups plus *Mastacembelus stappersii* and *Mastacembelus congicus,* plates are absent in African mastacembeloids. The best developed epibranchial dentition occurs in the large, lacustrine, predatory species from Lake Tanganyika (e.g. *M. cunningtoni* and *M. moorii*). In these species the anteroventral edge of epibranchials 1 and 2 is expanded to form a wide bony lip, whose ventral surface supports a series of relatively large toothplates. In a large stained specimen of *M. cunningtoni* (Fig. 64) held at the BM(NH) the toothplate was considered by Nelson (1969: 497) to be fused to epibranchial 1. Close examination of this specimen showed that although the toothplate is indeed tightly connected to epibranchial 1, it can be stripped intact from the overlying bone. In another Tanganyikan species (*Mastacembelus micropectus* Fig. 65) the toothplates are inseparably fused to epibranchial 1.

The pharyngobranchial elements generally support the *fused toothplates* of the dorsal gill arches, and are arranged in a way similar to that described for *M. mastacembelus* (p. 26). A toothplate is generally fused to the ventral surface of pharyngobranchial 2 (as described

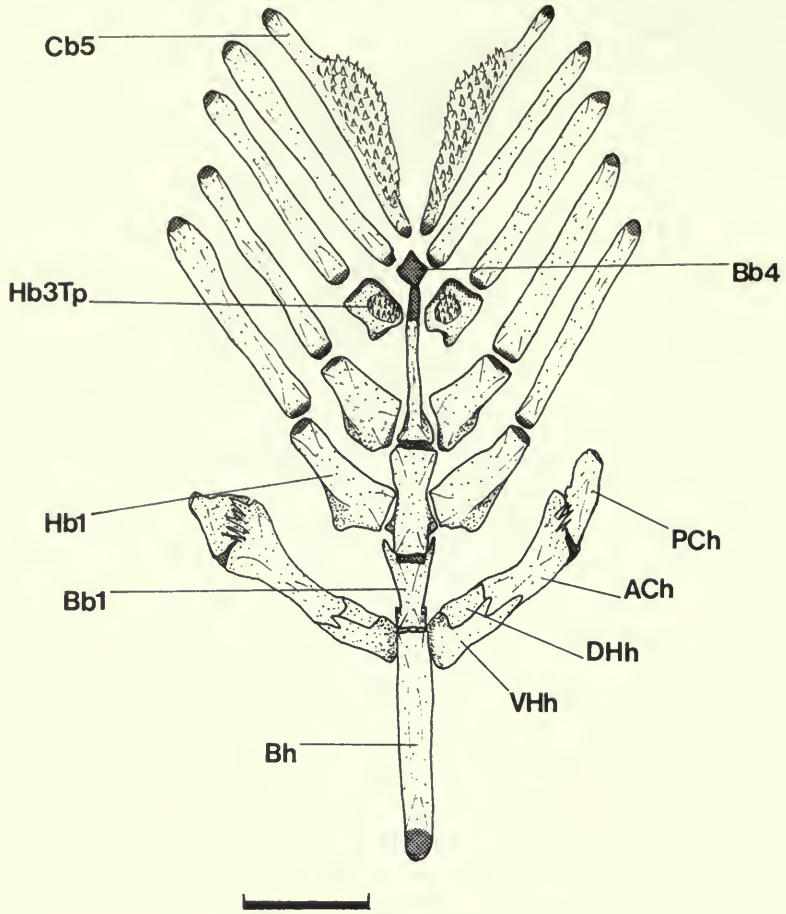


Fig. 62 *Mastacembelus flavomarginatus,* hyoid and lower gill arches in dorsal view.

in *M. mastacembelus* p. 27). Notable exceptions, which lack this toothplate, are the endemic lower Zairean rapids species (*M. paucispinis, M. brachyrhinus, M. brichardi, M. crassus* and *M. aviceps*), *M. marmoratus* and most west African taxa (*M. batesii, M. brevicauda, M. goro, M. greshoffi, M. liberiensis, M. loennbergii, M. longicauda, M. marchii* and *M. niger*). Prominent pharyngobranchial 3 and pharyngobranchial 4 toothplates are features of all mastacembeloids. The dentition on these toothplates, like that on the ventral plates, consists of relatively large caniniform teeth. On the unfused toothplates, the teeth are very much smaller and are usually conical, but are small and caniniform on the large toothplates occurring in the lacustrine species.

Pectoral girdle

The pectoral girdle shows remarkably few interspecific differences, either in overall proportions or in the shape of its constituent bones. The postcranial position of the girdle (adjacent to 3rd and 4th abdominal vertebrae) and the lack of a posttemporal bone connecting it to the neurocranium (as described in *M. mastacembelus* p. 27) are features common to all taxa.

Variation in the ventral limb of the *cleithrum* occurs among the Asian species. The cleithrum has a particularly deep ventrolateral face in *Mastacembelus zebrinus* (Fig. 67). Its ventromedial margin contacts its partner in a median symphysis and gives the pectoral girdle a 'keeled' ventral region. The depth of this keel increases both the surface area

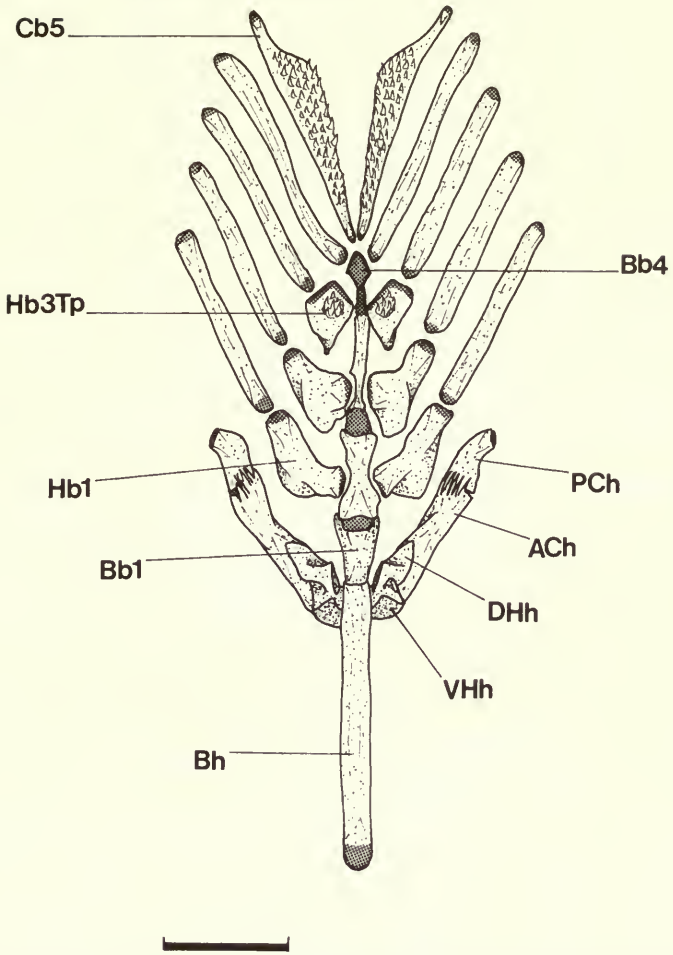


Fig. 63 *Mastacembelus liberiensis,* hyoid and lower gill arches in dorsal view.

available for muscle attachment, laterally, and that of the symphysis between the two halves.

The ventral limb of the cleithrum in *Mastacembelus pancalus* (Fig. 68a) and in the *Macrognathus* species (Fig. 68b) is also deep but proportionally less so than in *M. zebrinus.* The strengthening effect derived from expansion in this region of the girdle may be related to burrowing habits, and in particular the type of burrowing mechanism employed by these taxa (see Part II; Travers, 1984).

A cleithrum with a short, indistinct ventral limb occurs in a number of African taxa including *Mastacembelus brichardi, M. crassus, M. aviceps* (Fig. 69a) from the lower Zairean rapids; *M. micropectus* and *M. plagiostomus* (Fig. 69b) from Lake Tanganyika. In these species the ventral limb of the cleithrum is shallow and this, together with its slight anteroventral curvature, gives the bone a relatively straight overall shape. An accompanying tendency towards reduction of pectoral fin size occurs in these taxa.

The dorsal edge of the cleithrum is serrated in the undescribed *Mastacembelus* species (Fig. 70), *M. nigromarginatus* (Fig. 72) and *M. stappersii*; this contrasts with the smooth edge found in the majority of species.

A postcleithrum is absent in all mastacembeloids.

The *scapula* is pierced by a large foramen which is completely bone enclosed in all Asian taxa as shown for example in *Mastacembelus mastacembelus* (Fig. 11) and the *Macro-*

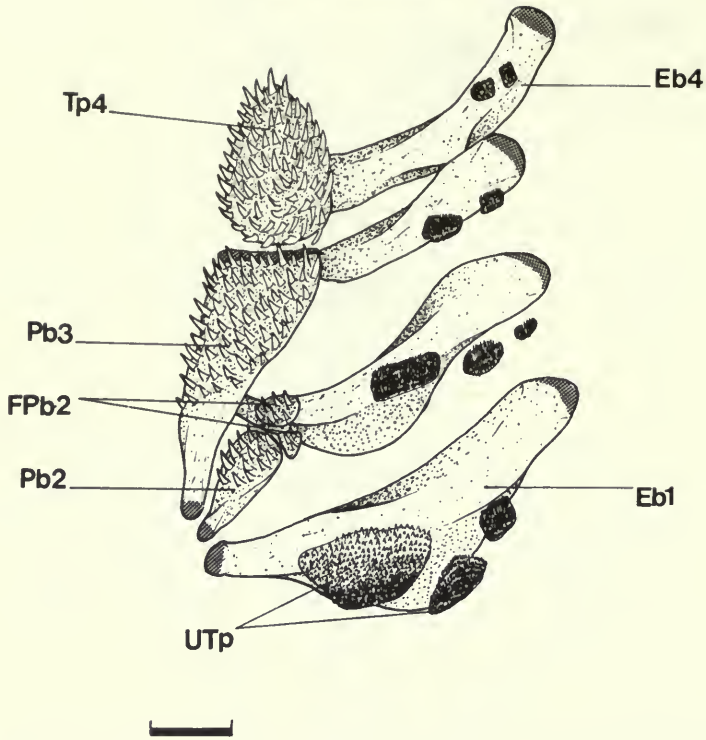


Fig. 64 *Mastacembelus cunningtoni,* upper gill arches; ventral aspect, right side.

gnathus species (Fig. 68b). The anterior edge of the foramen in the majority of African species, however, lies across the anterolateral margin of the bone and is enclosed by cartilage (see Figs 69, 70, 72 & 73).

Four, spool-shaped *radials* occur in all species. The two upper radials articulate with the posterior edge of the scapula, the third with the cartilage interface between it and the *coracoid,* and the fourth with the posterior edge of the coracoid (as described in *M. mastacembelus* p. 28). Radials with bifurcated (or even trifurcated) distal ends occur mosaically. The distal tips of all four radials are bifurcated in *Mastacembelus maculatus* and *M. greshoffi;* the 1st, 2nd and 3rd are bifurcated in *Macrognathus aculeatus* (Fig. 68b); the 2nd and 3rd in *Mastacembelus ophidium;* the 2nd in *M. loennbergii,* while the 2nd and 4th are trifurcated in *M. sinensis* and the 2nd is trifurcated in *M. liberiensis.*

The radials in a juvenile, 4 cm long, specimen of *M. maculatus* (Fig. 71) are cartilaginous and divided along most of their length (apart from the anterior ends), thus giving the appearance of 8 radials (i.e. the primitive teleostean complement: Jarvik, 1980). This suggests that the adult condition of 4 radials results from the fusion of neighbouring pairs of elements during ontogeny. In some cases each pair remains incompletely fused in the adult.

There are interdigiting processes between the radials in *Mastacembelus nigromarginatus* (Fig. 72), whilst in *M. zebrinus, M. brachyrhinus* and the undescribed species the 1st and 2nd radials are coalesced. Such radial fusion also occurs in some *M. tanganicae,* but in other specimens the 1st and 2nd radials are separate, indicating that this feature may be intraspecifically variable. The fusion between radials, the presence of interdigitating processes and, in some specimens, the coalescence of certain radials are all possibly associated with strengthening the pectoral fin base.

The 22 *pectoral fin rays* in *Mastacembelus mastacembelus* (p. 28) are intermediate in number between the highest (26 in *Mastacembelus oatesii*) and lowest (6 in the very small pectoral fin of *Mastacembelus micropectus*; in one individual they are completely lacking).

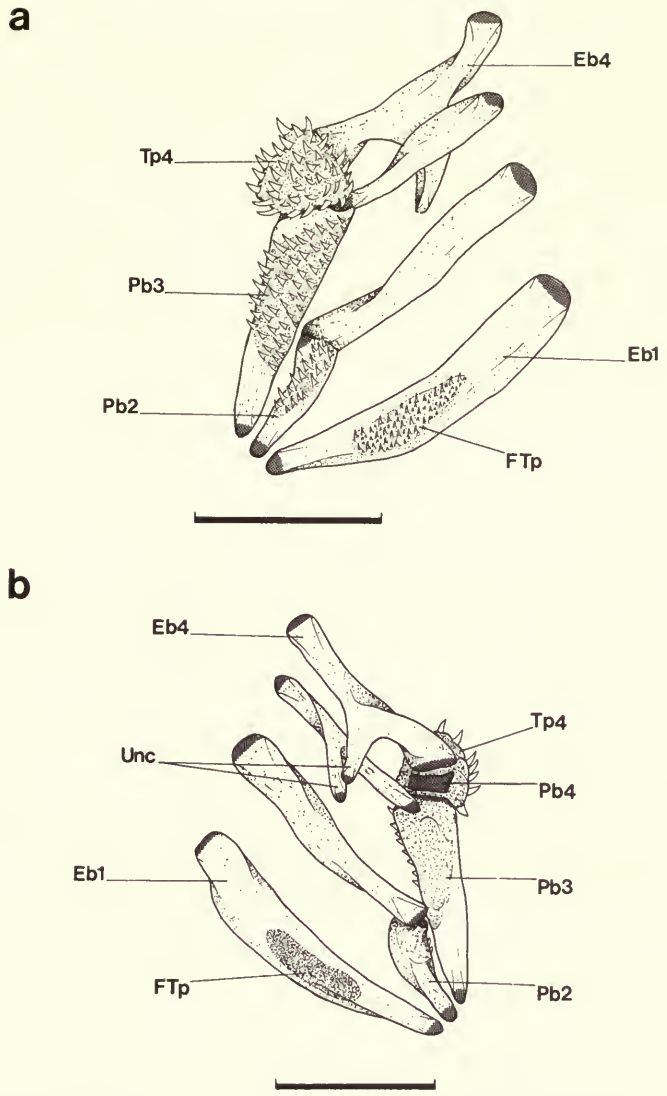


Fig. 65 *Mastacembelus micropectus,* upper gill arches (a) ventral aspect, (b) dorsal aspect; right side.

The pelvic girdle is absent in all mastacembeloids, and apart from *Mastacembelus longicauda* (Fig. 73), no pelvic elements remain. In a specimen of this species a pair of splinter-like bones lie longitudinally between the cleithra and are thought to represent basipterygia.

Vertebral column

There is only slight interspecific variation in the morphology of the *abdominal* and *caudal* vertebrae. The vertebral elements described in *M. mastacembelus* (p. 29) are, in general, typical for most taxa. A hemispherical condyle on the first abdominal centrum (Fig. 12) is present in all mastacembeloids. Wide, laterally compressed neural spines occur on the anterior abdominal vertebrae. These are confined to the first four vertebrae in *M. mastacembelus* (Fig. 12), and in most Asian forms, although the first 6 vertebrae have wide spines in all *Macrognathus* species, and only the first 2 in *Pillaia* (Fig. 21bii).

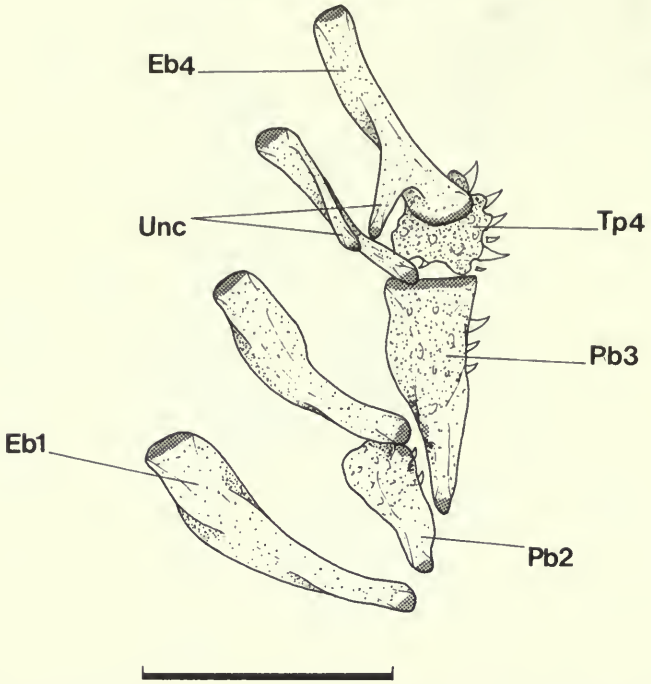


Fig. 66 *Mastacembelus sinensis,* upper gill arches; dorsal aspect, right side.

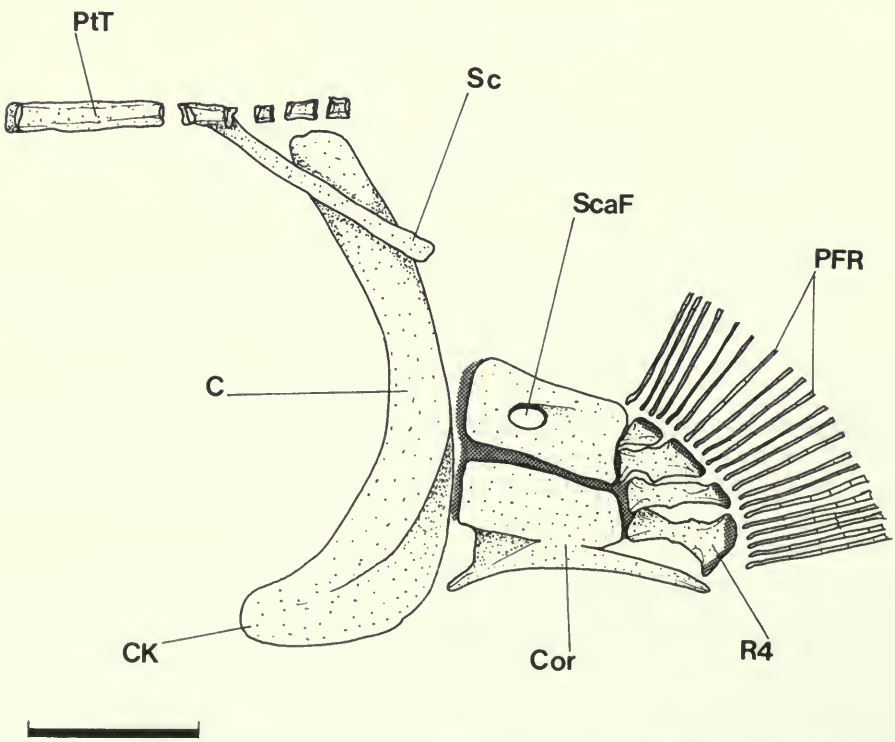


Fig. 67 *Mastacembelus zebrinus,* pectoral girdle; lateral aspect, left side.

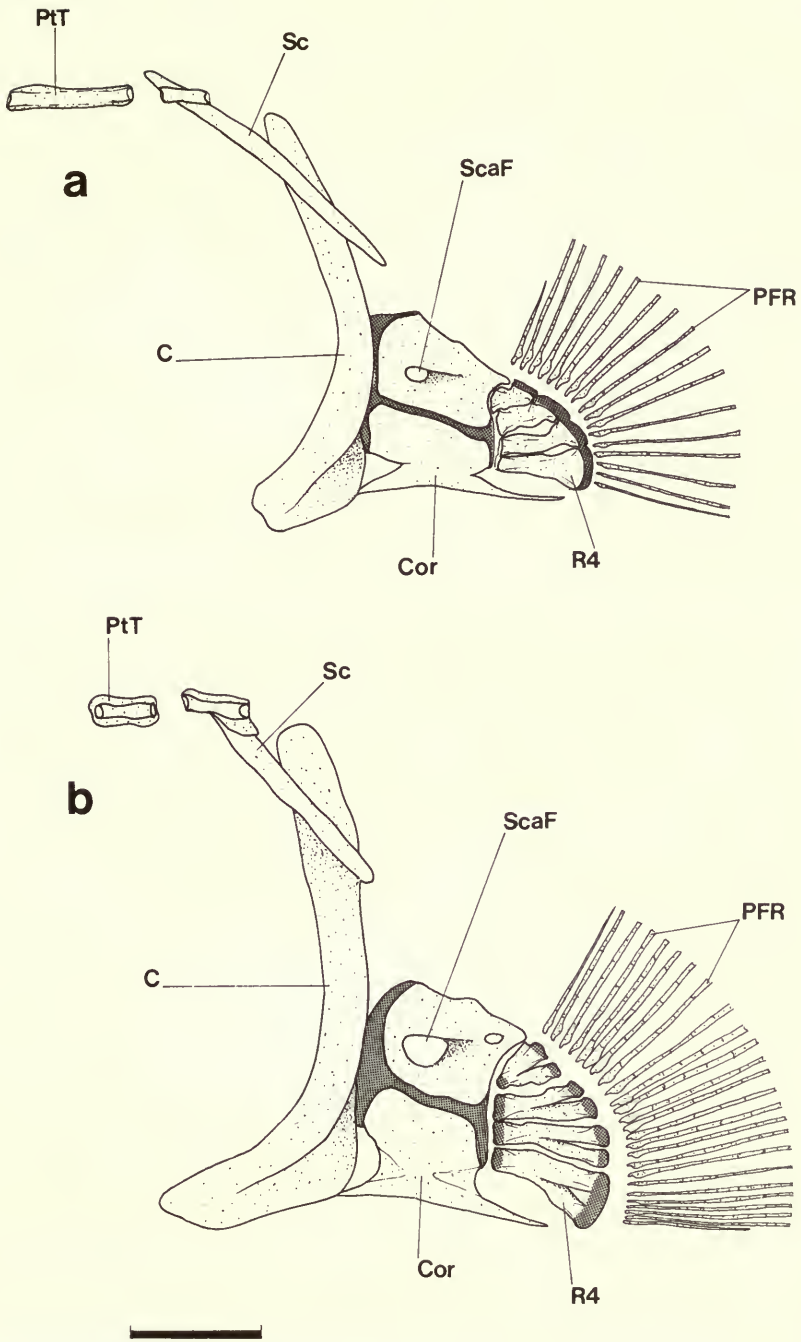


Fig. 68 Pectoral girdle in (a) *Mastacembelus pancalus*, and (b) *Macrognathus aculeatus*; lateral aspect, left side.

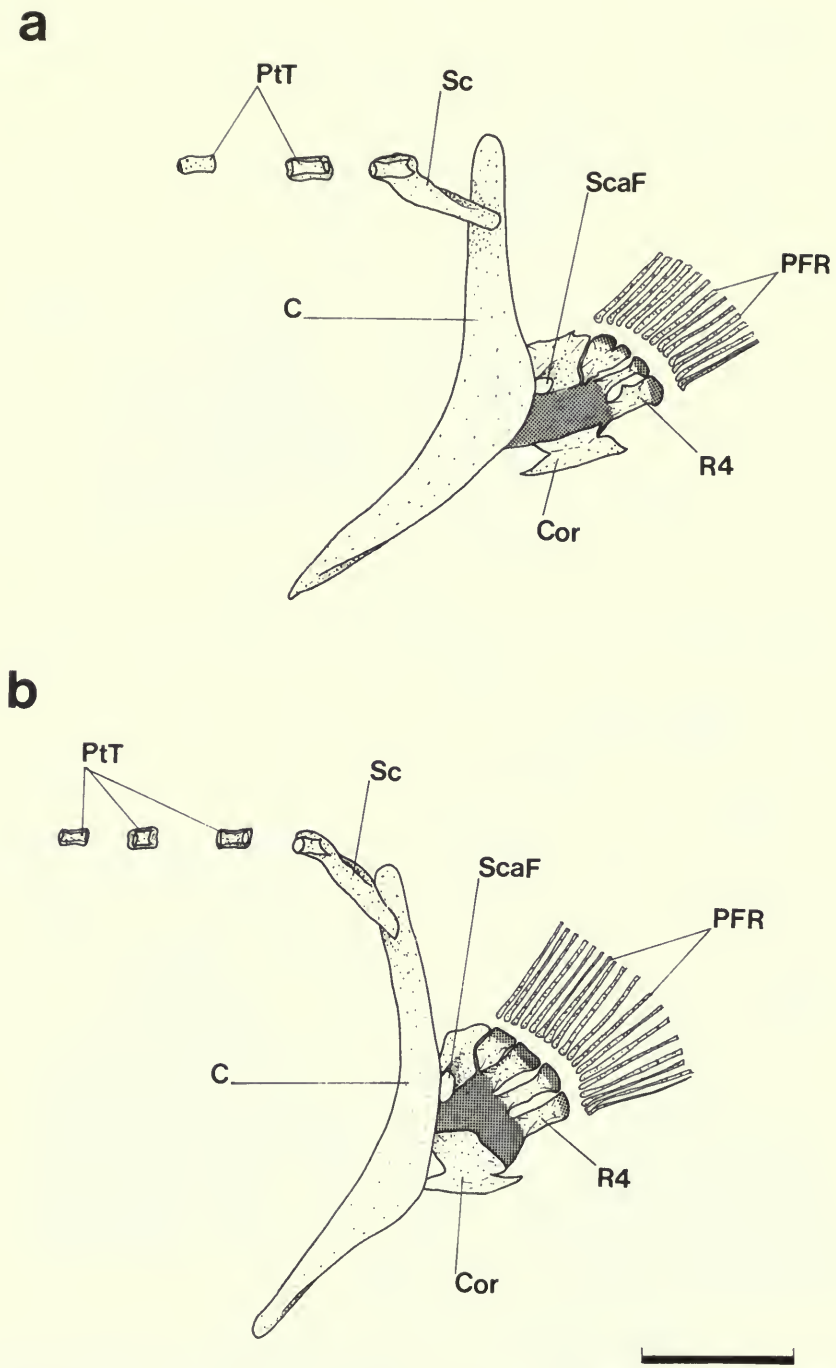


Fig. 69 Pectoral girdle in (a) *Mastacembelus aviceps*, and (b) *Mastacembelus crassus*; lateral view, left side.

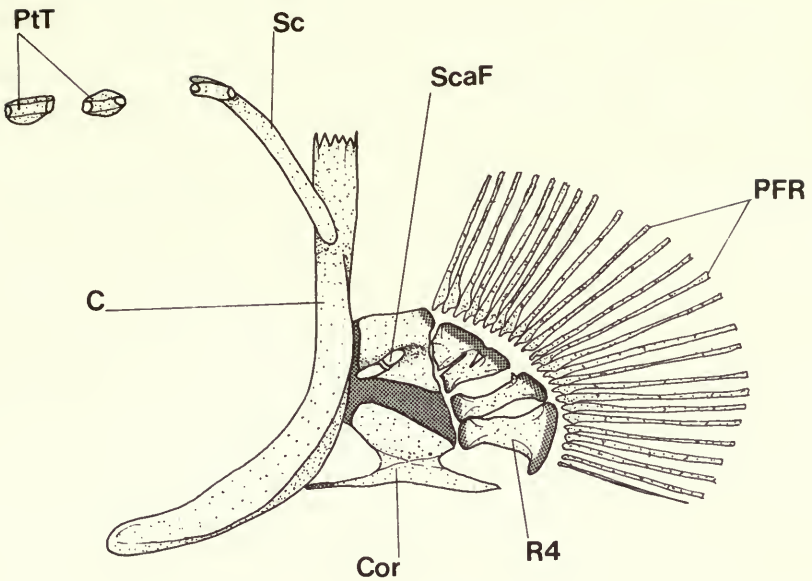


Fig. 70 Pectoral girdle in the undescribed *Mastacembelus* species; lateral aspect, left side.

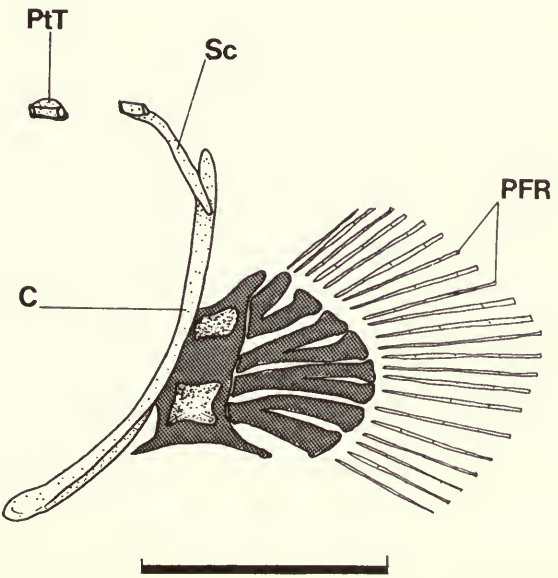


Fig. 71 Juvenile *Mastacembelus maculatus* (S.L.4 cm.) pectoral girdle; lateral aspect, left side.

In the African species wide neural spines are typically developed on the first 5 or 6 abdominal vertebrae. The first 8 vertebrae have wide neural spines in the west African *Mastacembelus loennbergii* and *M. reticulatus* and there are 9 such spines in *M. marmoratus* from Congo.

Anteroposteriorly expanded neural and haemal spines may also occur and are particularly prominent on all posterior caudal vertebrae in the 4 lacustrine species, *Mastacembelus ellipsifer, M. frenatus, M. moorii* and *M. ophidium* (discussed below). Elongated, narrow

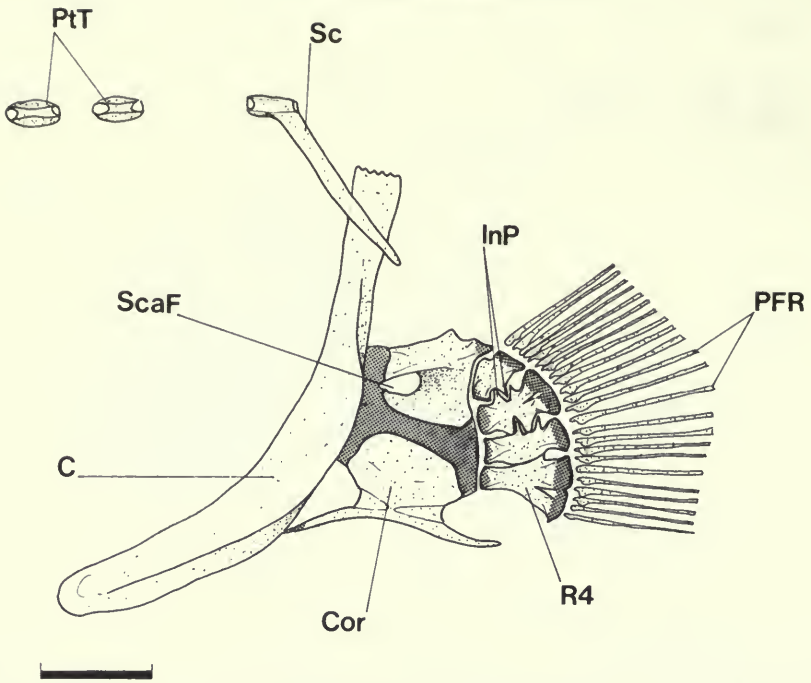


Fig. 72 *Mastacembelus nigromarginatus,* pectoral girdle; lateral view, left side.

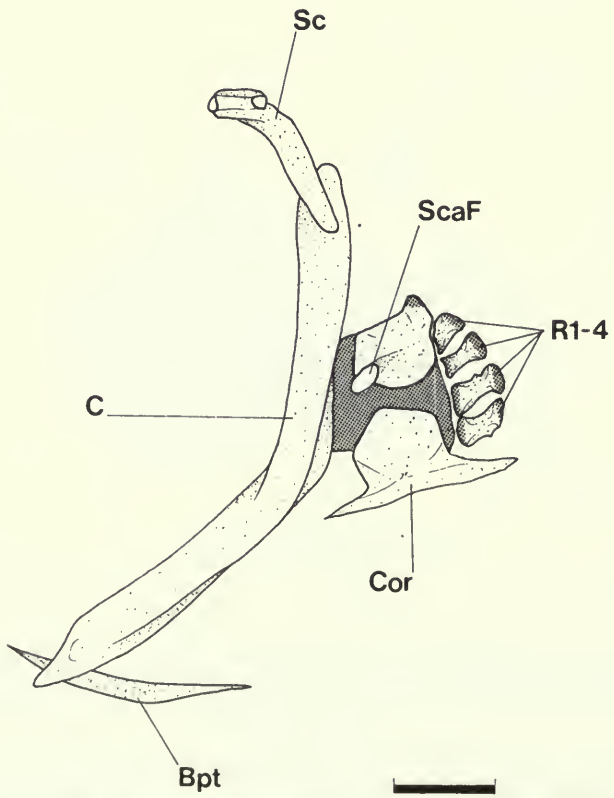


Fig. 73 *Mastacembelus longicauda,* pectoral girdle; lateral aspect, left side.

neural and haemal spines are found in some Asian taxa, including *Mastacembelus pancalus, M. zebrinus, M. keithi, M. caudiocellatus* and *Macrognathus* species (see Part II). The length of their spines gives these taxa a characteristic deep-bodied appearance.

The asymmetry of the centra as described in *M. mastacembelus* (p. 30) is a feature common to all Asian and African taxa examined.

The trend towards elongation, manifest by the skull, is continued postcranially by the relatively high numbers of abdominal and caudal vertebrae. The emphasis on elongation of the body in these taxa, through an increase in the number of vertebrae, is also associated with considerable interspecific variation in the numbers of abdominal and caudal vertebrae (Table 5). The number of abdominal vertebrae in *M. mastacembelus* is 38 (p. 29) and is modal for the majority of Asian and African species.

The lowest number of abdominal vertebrae recorded in any taxon is 25, in *Chaudhuria* and *Mastacembelus aviceps* and the highest 42, in *M. batesii.* The caudal vertebrae show a greater difference between their minimum, (36 in *M. pancalus*) and maximum (70 in *Mastacembelus liberiensis*) numbers. Many Asian taxa are distinguished by their relatively low number of abdominal and caudal vertebrae (see Table 5). These include *Mastacembelus pancalus* and to a lesser extent *M. zebrinus, M. keithi* and *M. caudiocellatus* and the *Macrognathus* species. These species are also outstanding among the mastacembeloids for the relatively greater length of their haemal and neural spines.

A low vertebral count also distinguishes a number of African species including *Mastacembelus albomaculatus, M. micropectus, M. plagiostomus, M. platysoma, M. tanganicae* and *M. zebratus* from Lake Tanganyika, and *M. brachyrhinus, M. brichardi, M. crassus* and *M. aviceps* from the lower Zairean rapids. The low vertebral number in these species is associated with other reductional trends seen in the rapids fishes and the crevice-living Tanganyikan species.

Other Tanganyikan species have a high vertebral count e.g. *Mastacembelus cunningtoni, M. ellipsifer, M. moorii,* and *M. ophidium,* as do many non-Tanganyikan species e.g. *M. liberiensis, M. longicauda, M. loennbergii, M. ansorgii* and *M. cryptacanthus,* and to a lesser degree such forms as *M. paucispinis* and the new species (Table 5). These taxa are distinguished by the marked difference between the number of abdominal and caudal vertebrae, and in having a long and tapered body. In some of these species (*M. moorii, M. ophidium, M. ellipsifer,* and also in *M. frenatus*) the neural and haemal spines on the posterior caudal vertebrae (as many as the last 25) are wide and blade-like.

On several occasions *Mastacembelus moorii* was observed swimming at approximately 10–15 m above the substrate in Lake Tanganyika (pers. obs.) and the unusual condition of the neural and haemal spines on its caudal vertebrae may possibly be a modification related to its habit of midwater swimming.

The endemic Lower Zaire River mastacembeloid fauna shows a reversal of the general trend towards a greater number of caudal vertebrae seen in the African mastacembeloids. Among these Zairean species there is a decrease in numbers of caudal vertebrae from 53 in *M. paucispinis* to 38 in *M. aviceps.*

Epicentral ribs occur on only the first vertebra in *Chaudhuria* (Fig. 21aii) and *Pillaia* (Fig. 21bii), but apart from these taxa are generally found in the arrangement described in *M. mastacembelus* (p. 29).

Epipleural ribs are confined to the fourth abdominal vertebra in *M. mastacembelus* (Fig. 12), an arrangement found in most Asian species although they are present on the third abdominal vertebra in *Mastacembelus sinensis,* and are absent in *Chaudhuria* and *Pillaia.* In the majority of African taxa epipleural ribs are confined to the fourth or fifth abdominal vertebra, but in a number of species from Lake Tanganyika, Zaire and West Africa they are absent.

Interspecific variation in the *pleural ribs,* apart from slight variation in length, is limited to differences in the point at which the ribs first appear. Pleural ribs are absent from the first 3 abdominal vertebrae in *M. mastacembelus* (Fig. 12), and this arrangement is typical for most Asian taxa as well, although in *Mastacembelus sinensis, M. pancalus* and *M.*

Table 5 Number of vertebrae, spinous and branched rays in mastacembeloid taxa.

	Vertebrae		Spinous rays		Branched rays	
	Abdominal	Caudal	Dorsal	Anal	Dorsal	Anal
Oriental mastacembeloid taxa						
Mastacembelus alboguttatus	38	47	37	3	84	83
Mastacembelus armatus	38	50	34	3	78	80
Mastacembelus caudiocellatus	37	44	34	3	68	68
Mastacembelus circumcinctus	30	47	28	3	59	68
Mastacembelus erythrotaenia	38	45	32	3	73	67
Mastacembelus guentheri	38	51	35	3	69	72
Mastacembelus keithi	31	42	32	3	54	59
Mastacembelus maculatus	32	44	26	3	56	61
Mastacembelus mastacembelus	38	47	35	3	73	75
Mastacembelus pancalus	28	36	25	3	36	41
Mastacembelus sinensis	36	44	33	3	68	65
Mastacembelus unicolor	38	48	35	3	74	77
Mastacembelus zebrinus	32	42	31	3	56	58
Macrognathus aculeatus	32	38	14	3	51	51
Macrognathus aral	32	39	21	3	55	54
Macrognathus siamensis	35	40	15	3	60	58
Chaudhuria caudata	25	46	Absent		40	42
Pillaia indica	28	37	Absent		34	36
African mastacembeloid taxa						
Mastacembelus albomaculatus	38	44	37	3	65	64
Mastacembelus ansorgii	37	63	32	3	111	102
Mastacembelus aviceps	25	38	22	2	47	52
Mastacembelus batesii	42	54	33	2	78	78
Mastacembelus brachyrhinus	33	45	31	3	68	72
Mastacembelus brevicauda	40	58	30	2	86	97
Mastacembelus brichardi	32	42	29	3	57	61
Mastacembelus congicus	34	53	29	3	85	91
Mastacembelus crassus	22	44	19	2	52	61
Mastacembelus cryptacanthus	38	65	34	2	118	125
Mastacembelus cunningtoni	33	56	30	3	88	90
Mastacembelus ellipsifer	36	52	33	3	83	86
Mastacembelus flavidus	38	58	37	3	85	75
Mastacembelus flavomarginatus	39	50	27	2	75	85
Mastacembelus frenatus	40	55	35	3	78	77
Mastacembelus goro	40	49	31	3	69	72
Mastacembelus greshoffi	39	56	30	2	130	122
Mastacembelus liberiensis	33	70	28	3	131	124
Mastacembelus loennbergii	38	63	30	2	123	125
Mastacembelus longicauda	38	66	27	3	114	120
Mastacembelus marmoratus	39	50	31	3	70	66
Mastacembelus micropectus	32	50	30	3	72	78
Mastacembelus moorii	33	63	28	3	110	102
Mastacembelus niger	40	51	29	3	74	73
Mastacembelus nigromarginatus	37	56	29	2	91	82
Mastacembelus ophidium	29	66	27	1	104	108
Mastacembelus paucispinis	28	53	9	3	120	85
Mastacembelus plagiostomus	40	48	33	3	59	66
Mastacembelus platysoma	29	42	25	3	66	63
Mastacembelus reticulatus	40	56	30	2	95	92
Mastacembelus sclateri	32	52	26	3	73	75
Mastacembelus shiranus	34	49	29	3	79	86

Table 5 Continued.

	Vertebrae		Spinous rays		Branched rays	
	Abdominal	Caudal	Dorsal	Anal	Dorsal	Anal
Mastacembelus signatus	32	54	29	3	80	82
Mastacembelus stappersii	38	58	33	3	82	87
Mastacembelus tanganicae	39	48	42	3	67	73
Mastacembelus vanderwaali	32	50	24	3	64	65
Mastacembelus zebratus	28	44	26	3	52	56
Mastacembelus sp. nov.	32	56	15	3	112	95

N.B. Numbers shown do not represent statistical samples. For mean number of vertebrae, spinous and branched rays in Oriental *Mastacembelus* species see Sufi, 1956; for frequency distribution of vertebrae and dorsal spinous rays in *Macrognathus* species see Roberts, 1980.

maculatus ribs are only absent on the first 2 vertebrae. In the African taxa pleural ribs tend to be absent from the first 3 or 4 vertebrae, although they are wanting on the first 5 centra in *M. frenatus, M. platysoma, M. vanderwaali* and *M. ubangensis.*

The greatest reduction in the number of pleural ribs, however, is seen in members of the Tanganyikan and Zairean faunas. In these species ribs are absent from as many as the first 20 abdominal vertebrae e.g. *M. albomaculatus* (16), *M. moorii* (16) and *M. micropectus* (14) from Lake Tanganyika, and *M. brachyrhinus* (20), *M. brichardi* (18), *M. crassus* (16) and *M. aviceps* (15) from the lower Zairean rapids.

Dorsal and anal fins

The morphology of the spinous and branched rays, and their supporting pterygiophores is constant in the mastacembeloids but there is considerable inter- and intra-specific variation in the total numbers of these elements (see Table 5 and Sufi, 1956 for morphometric data of Oriental species).

A long row of isolated *dorsal spinous rays* occurs in most mastacembeloids. In *M. mastacembelus* 35 spines extend from the level of the fourth abdominal to the third caudal vertebrae. This posterior extension of the spines across the abdominal/caudal vertebral junction is a common mastacembeloid feature.

Mastacembelus mastacembelus and several other Asian species (including *M. alboguttatus, M. armatus, M. erythrotaenia, M. oatesii* and *M. unicolor*) have high numbers of dorsal spines compared with the number in most Asian taxa (see summary of fin-ray numbers in Sufi, 1956: 108). A low number of spines does not appear to be related to the number of abdominal vertebrae (see below).

The *Macrognathus* species are distinguished from other Asian mastacembeloids by their relatively few dorsal spines; 21 in a specimen of *M. aral,* 15 (plus 1 predorsal; discussed below) in a specimen of *M. siamensis* and 14 in a specimen of *M. aculeatus* (see Roberts, 1980, table 2 for frequency distributions of dorsal spine counts in *Macrognathus*). Although, this number is under half that in *M. mastacembelus,* and although *Macrognathus* does not have significantly fewer abdominal vertebrae or vertebrae of significantly different proportions, the dorsal spines in all *Macrognathus* species also extend across the abdominal/caudal vertebral junction. Consequently, dorsal spines are not present above the anterior abdominal vertebrae, a characteristic feature of *Macrognathus* species. Spines are absent from above the first 18 abdominal vertebrae in the specimens of *M. aculeatus* and *M. siamensis* examined and from above the first 13 abdominal vertebrae in the specimen of *M. aral* (Roberts, 1980 also gives the frequency distributions of predorsal vertebral counts in *Macrognathus*; his table 4).

Dorsal and anal spines are absent in *Chaudhuria* and *Pillaia.*

Twenty-five to 35 dorsal spines are present in the majority of African species (Table 5). Two members of the Tanganyikan fauna (*Mastacembelus albomaculatus* and *M. flavidus*) have 37 dorsal spines, and a third species, *M. tanganicae* has 42, the maximum number found in any mastacembeloid.

The dorsal spines in the African species, regardless of their total number, originate from above the fourth, fifth or sixth abdominal vertebra, and extend across the abdominal/caudal vertebral junction.

Low numbers of dorsal spines are found in several of the rapids dwelling African species (see Table 5). *Mastacembelus paucispinis* (as its name implies), and the undescribed species, have exceptionally few, only 9 (plus 1 predorsal) occurring in *M. paucispinis* and 15 in the single specimen of the new species. Their spines extend posteriorly from above about the fourth or sixth abdominal vertebrae, but do not cross the abdominal/caudal vertebral junction. Associated with this exceptional arrangement of the dorsal spines there is a long rayed dorsal fin extending forward across the abdominal/caudal vertebral junction to a point close behind the last spine.

The low number of dorsal spines in *M. paucispinis* and the undescribed species may be the result of rays not developing into spines or the result of posterior spine loss (i.e. conversion of spines into rays; possibly a response to life in rapids), whereas, the small number in *Macrognathus* (where the spines lie posteriorly and cross the abdominal/caudal vertebral border) appears to be the result of anterior spine loss.

The first dorsal spine in *Mastacembelus ubangensis* and *M. marmoratus,* as well as in some West African species (e.g. *M. batesii, M. brevicauda, M. flavomarginatus, M. goro, M. loennbergii, M. longicauda M. niger* and *M. reticulatus*) is situated relatively far back along the vertebral column, at about the level of the ninth to twelfth vertebrae.

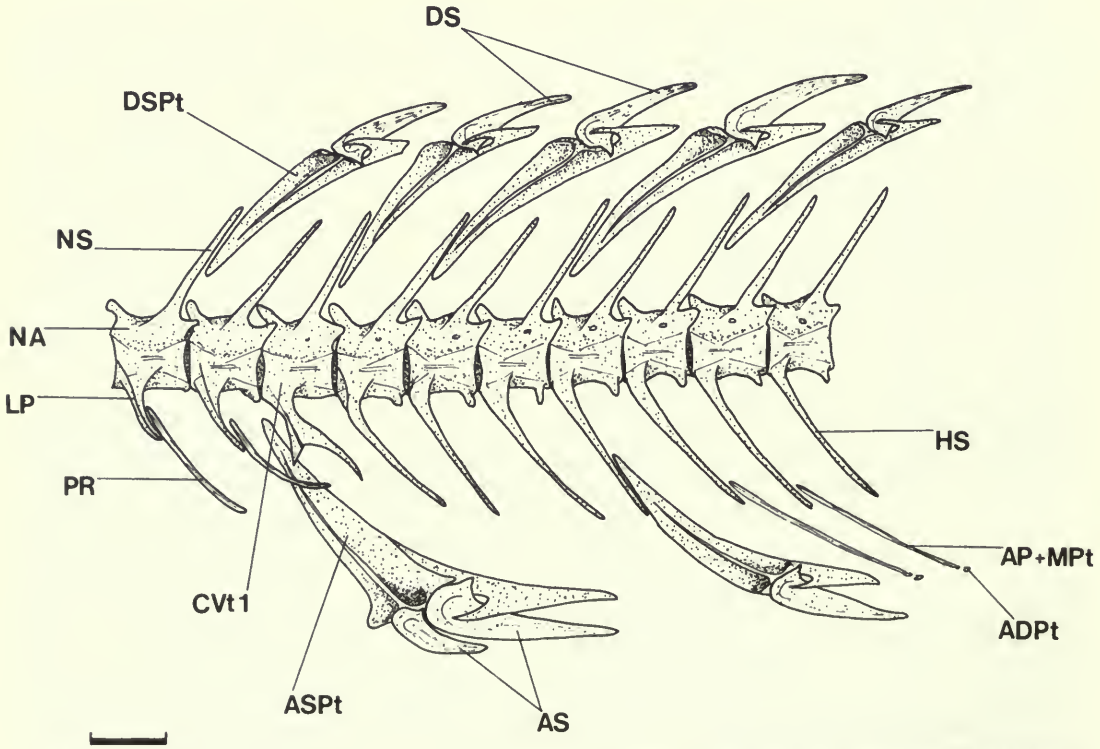


Fig. 74 *Mastacembelus sinensis,* abdominal/caudal vertebral junction and associated dorsal and anal spines; lateral view, left side.

Three *anal spinous rays* occur in all Asian mastacembeloids (apart from *Chaudhuria* and *Pillaia*).

The third anal spine in *M. sinensis* (Fig. 74) is equal in size to the large second anal spine. It is separated from that spine by a gap equal to 4 caudal vertebrae. This arrangement is atypical for the mastacembeloids and is found only in *M. sinensis*.

Three anal spines also occur in the majority of African taxa. However, a single spine is characteristic of *Mastacembelus ophidium,* and 2 anal spines occur in the Zairean rapids' species *M. crassus* and *M. aviceps,* and in a number of west African species including, *M. batesii, M. brevicauda, M. flavomarginatus, M. greshoffi, M. loennbergii, M. nigromarginatus* and *M. reticulatus* (Table 5).

A small bone (predorsal *sensu* Smith & Bailey, 1961), resembling the pterygiophore of a dorsal spine, is present anterior to the pterygiophore of the first dorsal spine in *Macrognathus siamensis* and in some African mastacembeloids includng *M. ophidium* among the Tanganyikan species, and *M. batesii, M. brevicauda, M. flavomarginatus, M. greshoffi, M. loennbergii, M. marmoratus, M. nigromarginatus* and *M. paucispinis* from western Africa.

Interspecific variation in the number of *branched fin rays* and their supporting *pterygiophores* is common. This variation may be directly related to the number of caudal vertebrae, as shown for example by *Mastacembelus liberiensis* which has the highest number of caudal vertebrae (i.e. 70) and also a high number of branched dorsal and anal fin rays (131 & 124, respectively). However, as a general rule, species total number of dorsal fin elements (spines and branched rays) are directly proportional to their total (abdominal and caudal) vertebrae number (see Table 5).

The development of spinous rays may influence the number of branch rays in the dorsal fin in some rapids dwelling species, as shown for example by *M. paucispinis* in which there are 9 dorsal spines, a moderate number of caudal vertebrae (53), but a high number of branched rays (120) which extend anteriorly across the abdominal/caudal vertebral junction. Apart from the undescribed species (p. 110), in no other mastacembeloid taxa were branched rays found to cross the abdominal/caudal vertebral junction.

There are relatively few branched dorsal and anal fin rays (generally not exceeding more than 60 elements) in *Macrognathus* species. *Mastacembelus pancalus* also exhibits a short dorsal and anal fin and has, apart from *Pillaia*, the smallest number of branched rays recorded in any mastacembeloid (36 dorsal and 41 anal) as well as a low number of spinous rays (25). The low number of dorsal fin elements (spines and rays) in these taxa can be directly related to their low total vertebral number (see Table 5) and anterior loss of spines (see p. 109).

Caudal fin

The caudal skeleton shows considerable inter- and intraspecific variation in the topography of its elements. The arrangement found in *M. mastacembelus* (p. 31) is more typical of the Asian than the African taxa.

To obtain an accurate appraisal of the caudal anatomy in a particular species a series of specimens was examined (where possible) in order to assay intraspecific variability. In most cases this had to be done with the aid of radiographs; it was thus not always possible to distinguish finer details (e.g. whether a uroneural is fused to or merely closely associated with the urostyle).

The caudal fin is distinct in the majority of Asian taxa (see Sufi, 1956), a feature distinguishing them from all African species, where the caudal fin is always confluent with the posterior branched rays of the dorsal and anal fins. In those Asian species which have the caudal united with the dorsal and anal fins (e.g. *Mastacembelus erythrotaenia, M. armatus, M. maculatus, M. caudiocellatus* and *M. circumcinctus*) the caudal rays are longer than, and extend beyond the tips of, the last dorsal and anal fin rays. Thus, in effect, a distinct caudal fin is discernible.

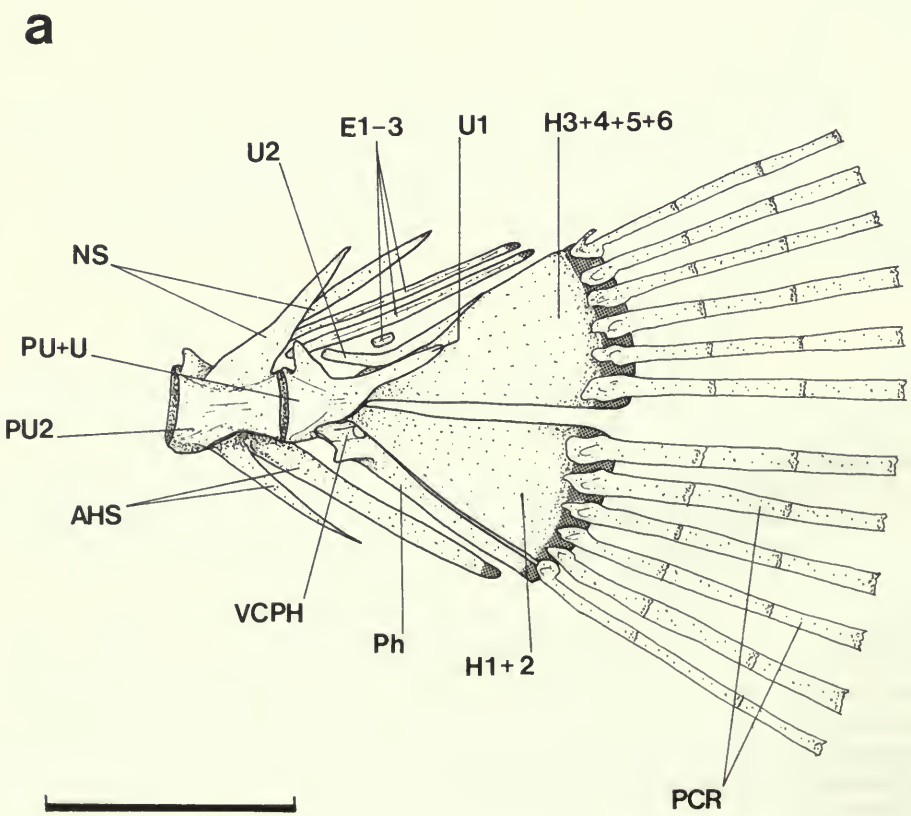
Associated with the distinct caudal fin of the Asian species is a relatively high number of principal *caudal rays* (usually about 16–20). *Mastacembelus pancalus* (Fig. 75a) is exceptional in having only 12 fin rays despite its having a distinct caudal fin.

The caudal in *M. sinensis, Chaudhuria* (Fig. 23a) and *Pillaia* (Fig. 23b) is also exceptional among Asian mastacembeloids since it is confluent with the dorsal and anal fins, and has only 8 or 9 rays. This arrangement is similar to that in the African taxa, all of which have a confluent caudal composed, in the majority of species, of 8–10 principal rays (see Figs 76, 77a & 78). Six principal caudal fin rays occur, however, in *Mastacembelus batesii, M. ophidium* and *M. aviceps,* whilst in *M. zebratus* there are only 4.

The number of *hypurals* varies from 5 autogenous elements to a single autogenous fan-shaped hypural plate. The size of the hypurals in taxa with 3 or 4 elements is proportionally smaller than in those with only 2 elements, and is probably the result of hypural fusion (faint suture lines can be seen in some cases e.g. *Mastacembelus congicus* Fig. 76b).

In the Asian species there are usually 4 or 5 hypural elements. This number is associated with the more distinct caudal fin and higher number of rays characterizing these taxa (see Figs 14, 75b & c). *Mastacembelus pancalus* (Fig. 75a) is exceptional in having only 2 large hypural elements (which may be correlated with the relatively low fin ray number i.e. 12) even though its caudal is distinct. Two hypural elements are otherwise found only in *M. sinensis, Chaudhuria* and *Pillaia.*

The majority of African mastacembeloids have only 2 distinct hypurals (Fig. 76a & b). Three hypurals are found only in *M. moorii* and in the undescribed species. A single fan-shaped hypural plate distinguishes *M. ellipsifer* (Fig. 77a) and *M. aviceps* (Fig. 77b) from all other African species.



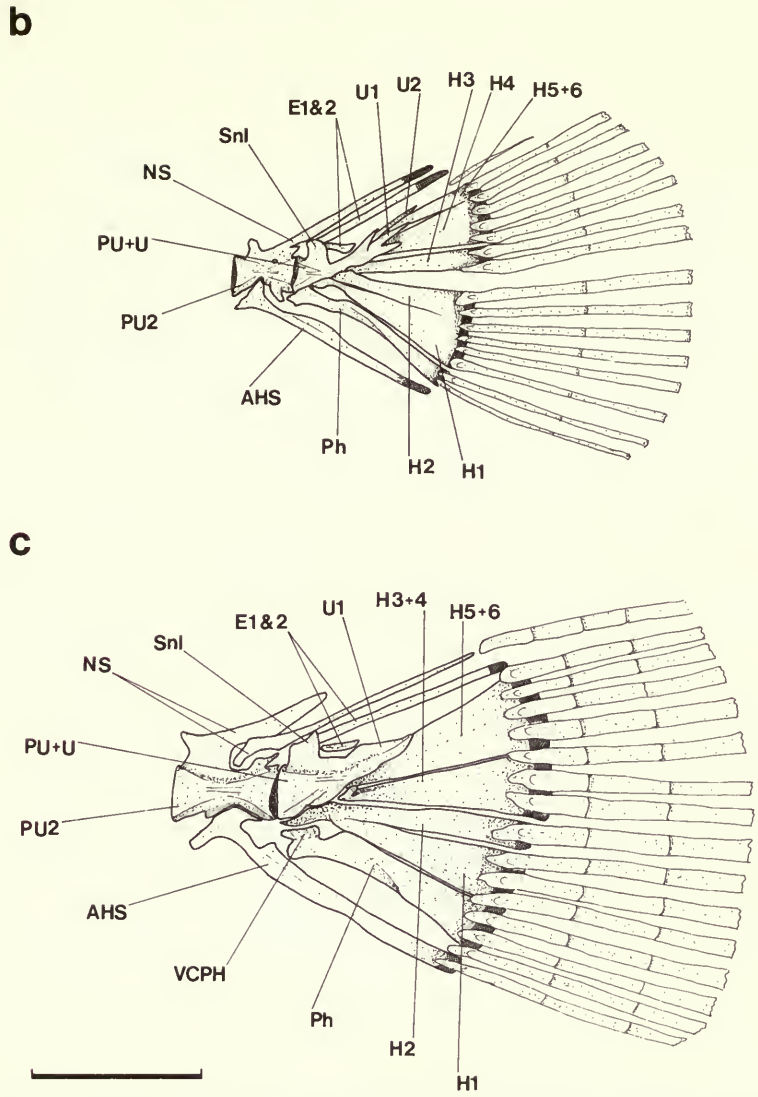


Fig. 75 Caudal fin skeleton in (a) *Mastacembelus pancalus,* (b) *Macrognathus aculeatus* and (c) *Mastacembelus erythrotaenia*; lateral aspect, left side.

The *parhypural* is autogenous and relatively large, compared with its condition in *M. mastacembelus*, in most taxa. It may become fused to the anterior edge of the first hypural in a number of African species (Fig. 78a & b).

Generally, there is only a single *uroneural* apparently fused along the dorsal edge of urostylar centrum, but it is not always possible to establish whether the uroneural is fused or merely closely associated with this centrum. In addition to this element, a single unfused uroneural (uroneural 2) occurs in *Macrognathus aculeatus* (Fig. 75b) and *Mastacembelus pancalus* (Fig. 75a), as well as in a variety of African species, including most of those in Lake Tanganyika. Two uroneurals were also found in two other species, *M. nigromarginatus* and *M. reticulatus,* both from West Africa. In many Asian and African taxa (including *M. maculatus, M. stappersii, M. niger* and *M. vanderwaali,* Fig. 76a), the uroneural has a bony extension developed from its upper margin, this is equivalent to the supraneural lamina discussed by Greenwood & Rosen (1971: 14).

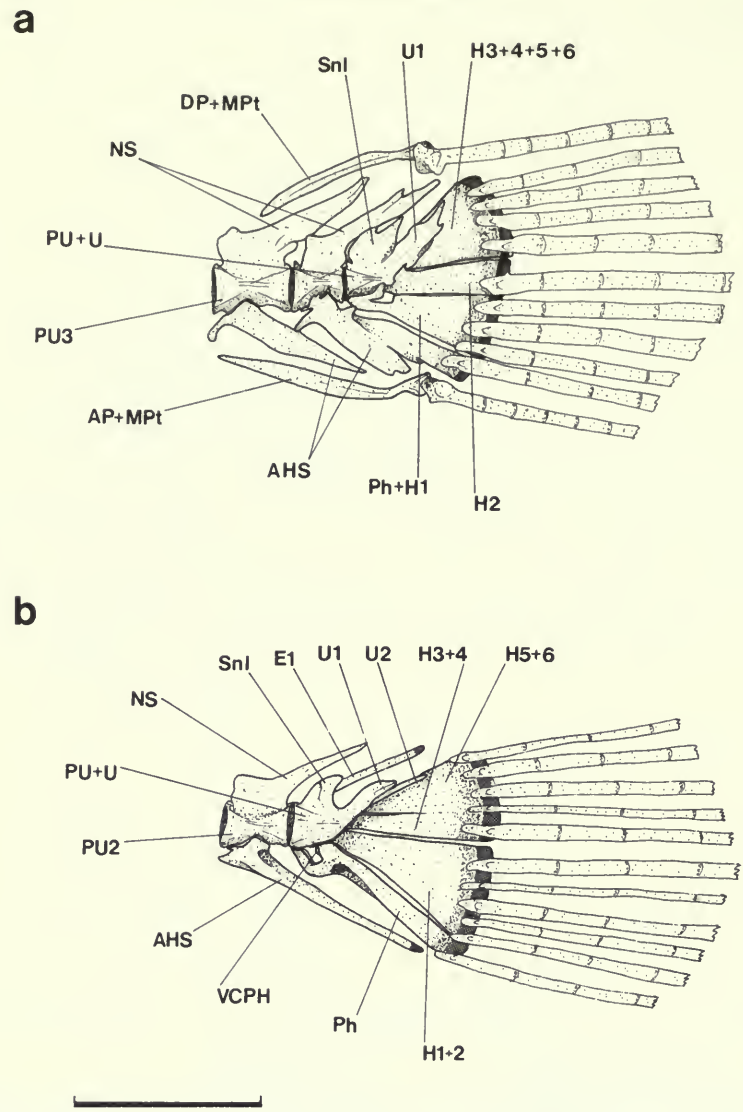


Fig. 76 Caudal fin skeleton in (a) *Mastacembelus vanderwaali* and (b) *Mastacembelus congicus*; lateral view, left side.

The number of *epurals* is also variable and ranges from a maximum of 3 to their total absence. Three epurals are found in *M. pancalus* (Fig. 75a) and *M. unicolor* but in no other species; 2 epurals occur in *M. erythrotaenia, M. guentheri* and *Macrognathus aculeatus* (Fig. 75b), with 1 in most of the remaining Asian taxa. The majority of African species have one or no epural, although *M. moorii,* and *M. nigromarginatus* have 2.

The *second preural vertebra* contributes to the caudal skeleton in a number of mastacembeloids. The haemal arch of this vertebra is autogenous in the majority of Asian taxa (*M. mastacembelus,* Fig. 14; *M. erythrotaenia,* Fig. 75c; and *Macrognathus* species, Fig. 75b). Its long haemal spine extends posteriorly to lie along the anterior edge of the parhypural, and its tip contributes to the support of the ventral caudal fin rays. In *Chaudhuria* (Fig. 23a) and *Pillaia* (Fig. 23b) the haemal arch is fused to the second preural vertebra and has a short haemal spine which does not contribute to the support of the caudal fin rays.

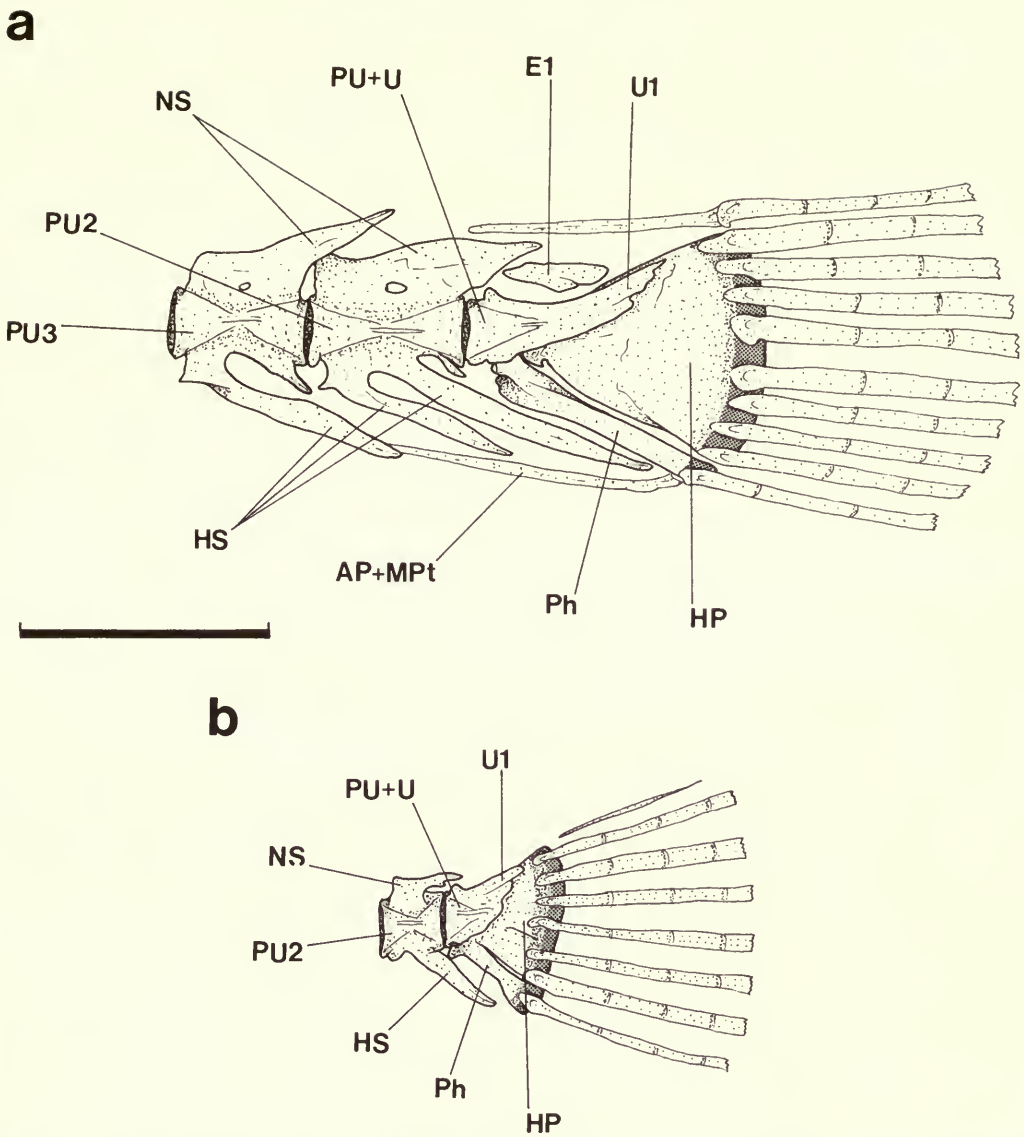


Fig. 77 Caudal fin skeleton in (a) *Mastacembelus ellipsifer,* and (b) *Mastacembelus aviceps*; lateral view, left side.

The haemal spine is short, non-ray supporting, and its arch fused to the second preural vertebra in the majority of African taxa (see Figs 76a, 77 & 78). In *Mastacembelus congicus* (Fig. 76b) however, the haemal spine is ray-supporting, and extends from an autogenous haemal arch in a manner similar to that of most Asian taxa.

Squamation

Small, *cycloid scales* cover the body, apart from the dorsal surface of the head in the majority of mastacembeloids. In some Asian taxa (e.g. *Mastacembelus pancalus*) the dorsal surface of the head is also covered in scales.

Chaudhuria and *Pillaia* among the Asian species, and *Mastacembelus latens,* (Roberts & Stewart, 1976: 307), *M. crassus,* and *M. aviceps* among the African taxa are completely scale-

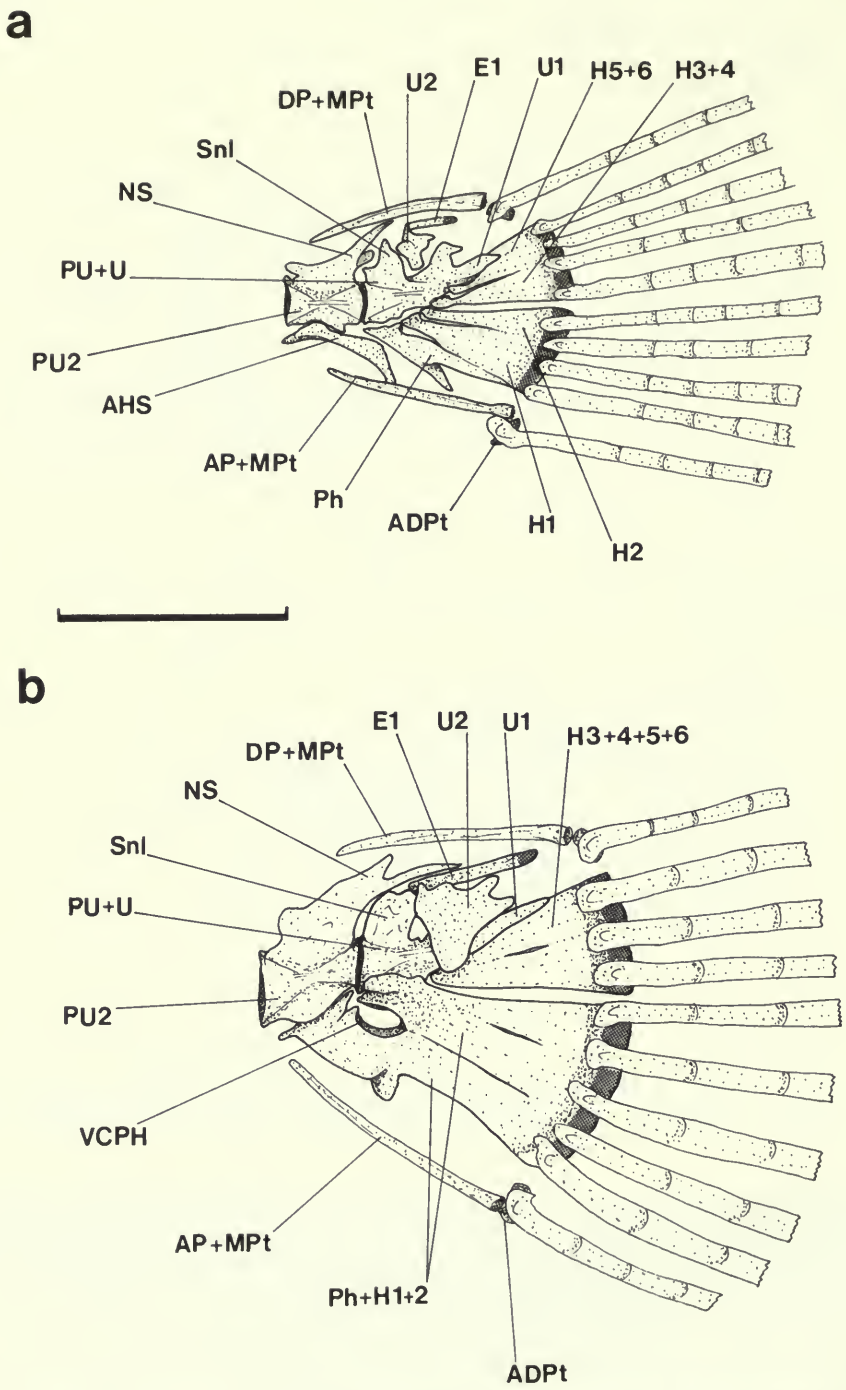


Fig. 78 Caudal fin skeleton in (a) *Mastacembelus shiranus* and (b) *Mastacembelus frenatus*; lateral aspect, left side.

less. An intermediate state between the modal condition and that found in these taxa occurs in *Mastacembelus micropectus.* Here, only the posterior third of the body is scaled.

Myology of *Mastacembelus mastacembelus*

Cephalic muscles

Group one muscles

The massive size of the adductor musculature, in comparison with the relatively small neurocranial, jaw and hyopalatine bones, is probably an indication that the mastacembeloid jaws are capable of powerful biting actions.

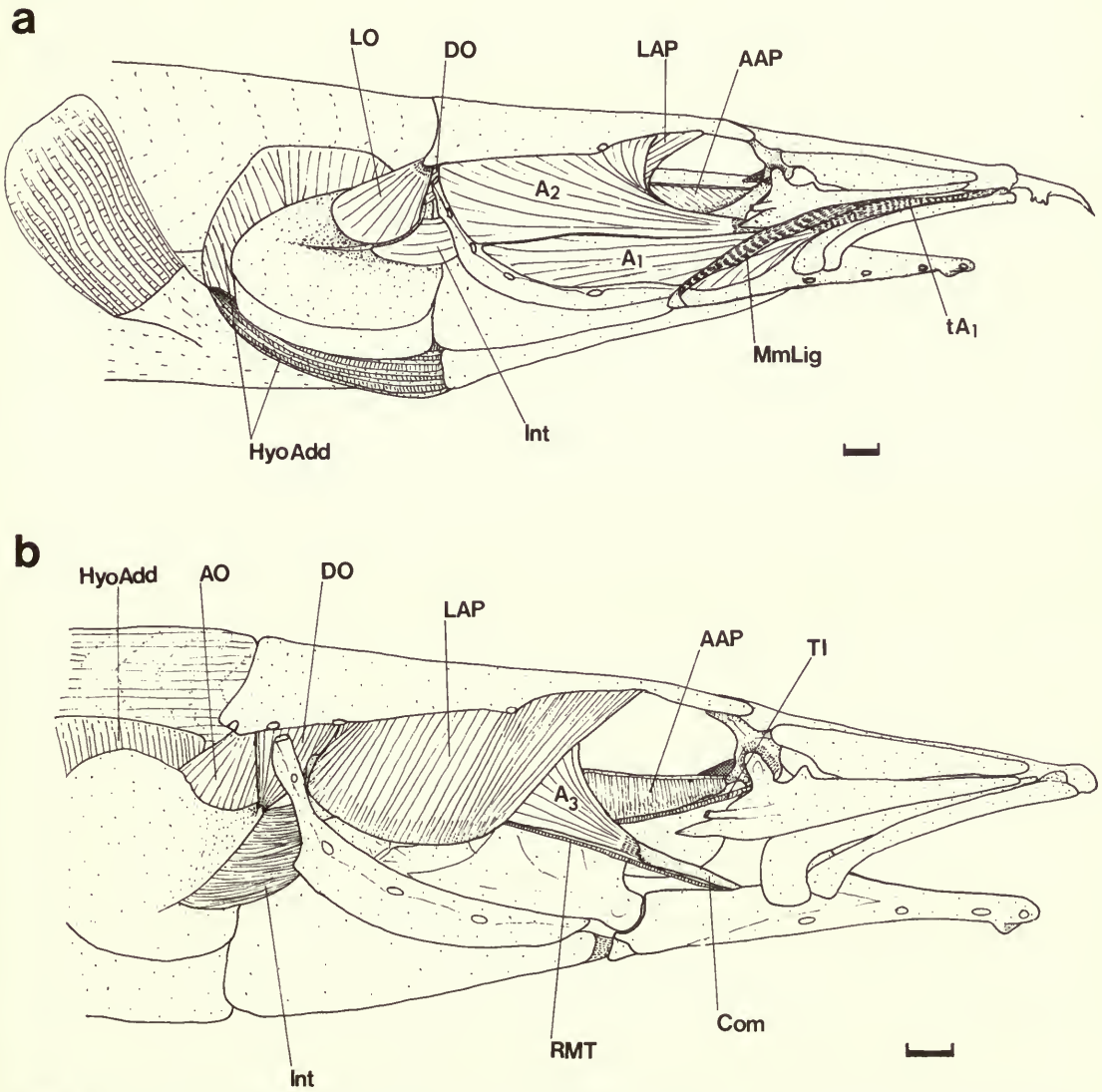


Fig. 79 *Mastacembelus mastacembelus,* (a) superficial cephalic muscles, tendons and ligament after removal of the skin and eyeball, and (b) deep cephalic muscles and tendons after removal of parts A_1 and A_2 of the *adductor mandibulae* muscle and the *levator operculi* muscle; lateral view, right side.

Four subdivisions of the *adductor mandibulae* (A_1; A_2; A_3 & A_w) are present in *Mastacembelus mastacembelus*. A ligament (Fig. 79a) passes superficially across the anterior region of the *adductor mandibulae,* from the lateral edge of the anguloarticular facet to the ventromedial face of the large 1st infraorbital bone. A small subdivision of this ligament passes from its ventral end below the adductor anterior tendon (tA_1) to attach to the mass of connective tissue on the posteromedial face of the maxilla (between it and the lateral face of the coronoid process). Although somewhat displaced, this ligament is thought to be homologous with the maxillo-mandibular ligament recently discussed by Stiassny (1981: 283).

Part A_1 of the *adductor mandibulae* (Fig. 79a) originates from the lateral face of the preoperculum (horizontal arm), symplectic, quadrate and posterolateral face of the anguloarticular. It is the smaller of the superficial adductor elements, and lies ventral to part A_2. A wide tendon (tA_1) extends anteriorly from the lateral face of A_1 and inserts along the ventrolateral margin of the maxilla and dorsal surface of the premaxilla. An inner slip of muscle fibres from the anteromedial face of A_1 insert musculously on the lateral face of the tendinous anterior end of the A_2 division.

Part A_2 forms the main mass of the superficial adductor musculature in *M. mastacembelus* (Fig. 79a). It lies dorsal to A_1 and curves anteriorly around the posteroventral edge of the orbit. The medial fibres of A_2 originate ventrally from the lateral face of the preoperculum (vertical arm), hyomandibula, symplectic, quadrate and coronomeckelian, and dorsally from the dorsolateral edge of the parietal, pterotic and frontal. A_2 is composed of two sections distinguished anteriorly by their separate tendons and sites of insertion. The upper section $A_{2\beta}$ (Fig. 79a) constitutes the bulk of the muscle, its fibres merging anteriorly onto a short, broad tendon that inserts on the posterodorsal edge of the coronoid process. The smaller lower section, $A_{2\alpha}$ (Fig. 80) has a narrow tendon which passes medially to merge with a wide aponeurosis on part A_w of the adductor complex.

The *truncus hyomandibularis* part of the VIIth cranial nerve emerges from the ventral hyomandibular foramen below the level of the dorsal margin of A_2 and runs anteriorly across its medial face before passing below the quadrate. A_2 is separated from the deeper part (A_3) of the *adductor mandibulae* by the *levator arcus palatini* muscle.

Part A_3 lies medial to the *levator arcus palatini* and is separated from it by a thin sheet of connective tissue. This broad muscle originates, ventrally, from the dorsolateral face of

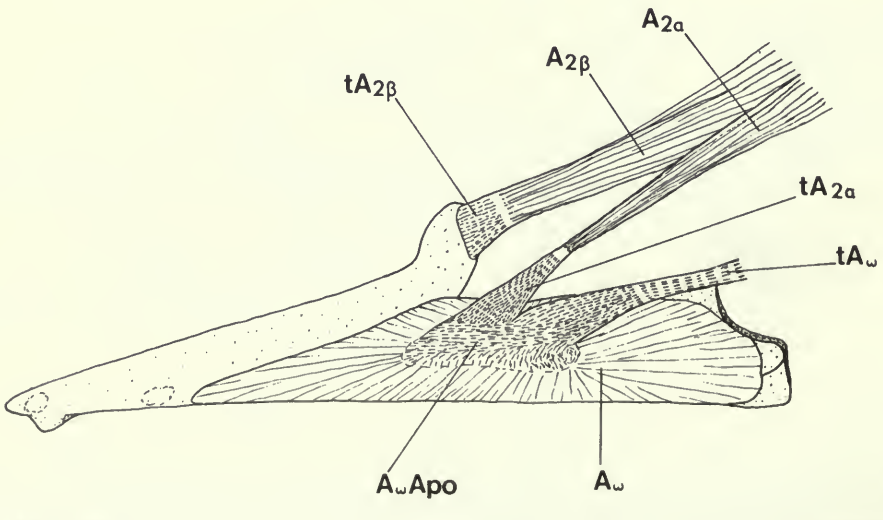


Fig. 80 *Mastacembelus mastacembelus,* lower jaw and associated musculature; medial aspect, right side.

the suspensorium (including the lateral face of the hyomandibula, quadrate, metapterygoid and endopterygoid) and dorsally from the precommissural lateral wall of the neurocranium (including the sphenotic, prootic, pterosphenoid and descending frontal lamina). The fibres course ventrorostrally, merging into a strong tendon (tA_3) that runs across the somewhat bulbous anterolateral face of the ectopterygoid (Fig. 79b). The tendon appears to have ossified in this region, possibly contributing to the unusually large coronomeckelian (Travers, 1984).

The anterior tip of the coronomeckelian is connected tendinously (tA_3) to the medial face of the meckelian fossa—along the posterodorsal edge of Meckel's cartilage. The *ramus mandibularis* of the trigeminal nerve branches from the *truncus infraorbitalis* medial to A_3, and passes ventrorostrally along the ventral edge of tA_3 and the long coronomeckelian.

Part A_w (Fig. 80) originates from the medial face of the mandible (including the anguloarticular, retroarticular and ventromedial margin of the dentary). Its fibres converge on a medial tendinous aponeurosis which is consolidated adjacent to the anguloarticular facet. This aponeurosis inserts on the anteromedial margin of the quadrate, just below the posteromedial process of the ectopterygoid.

The *levator arcus palatini* (Fig. 79b) is a thin sheet compressed between the dorsal region of A_2 and A_3; it originates along the dorsolateral edge of the neurocranium (pterotic and frontal), with its posterior fibres stemming from the postorbital process of the sphenotic.

The muscle runs vertically to insert musculously on the lateral face of the suspensorium, including the ventrolateral face of the hyomandibula and metapterygoid, and the dorsolateral face of the symplectic. It narrows posteriorly and its fibres intermix with the anterior fibres of the *dilatator operculi.*

The *dilatator operculi* (Fig. 79a) lies posterior to the *levator arcus palatini.* The lateral face of the dilatator is partly covered by the posterodorsal edge of *adductor mandibulae* A_2 and the upper arm of the preoperculum. It originates from the lateral face of the pterotic (above its hyomandibular fossa) and from the posterolateral margin of the sphenotic ventral to the postorbital process. Its fibres converge across the lateral face of the posterior hyomandibular condyle, and merge into a short tendon inserting firmly on the dorsal surface of a prominent dilatator process of the operculum.

Group two muscles

The *levator operculi* (Fig. 79a) is a comparatively large and ovoid muscle originating from the posterolateral face of the pterotic dorsal to the posterior end of the hyomandibular condyle. The dorsomedial face overlies the upper region of the *adductor operculi.* Ventral to this the medial face overlies the notched dorsal edge of the operculum, posterior to the opercular facet, and inserts musculously on the dorsolateral face of this bone. The ventral edge of the levator inserts along the narrow dorsal surface of the opercular ridge. This prominence separates it from a distinct muscle–the '*musculus intraoperculi*' (discussed below)–on the ventrolateral face of the operculum. The latter muscle originates on the posterolateral edge of the preoperculum, and inserts musculously on the adjacent lateral face of the operculum, ventral to the operculum ridge (Fig. 79a). There is no connection between this muscle and the *levator operculi* in *M. mastacembelus* (see p. 120).

The *adductor operculi* (Fig. 81) is a relatively small muscle covered, in lateral view, by the *levator operculi* and the operculum. It originates tendinously from the dorsolateral face of the exoccipital at a point below the posterior end of the pterotic facet for the hyomandibula. Its fibres expand ventrocaudally from a dorsal apex to insert musculously on the medial face of the operculum. The fibres along the posterior margin of the adductor intermingle with those from the dorsolateral region of the *hyohyoidei adductores* (discussed below). Between the anteromedial margin of the *adductor operculi* and the posterior edge of the *adductor hyomandibulae* is a pseudobranch (Bhargava, 1953). The buccal face of the pseudobranch lies just above the integumentary lining of the pharynx in a lateral recess in the dorsomedial face of the hyomandibula (Fig. 81).

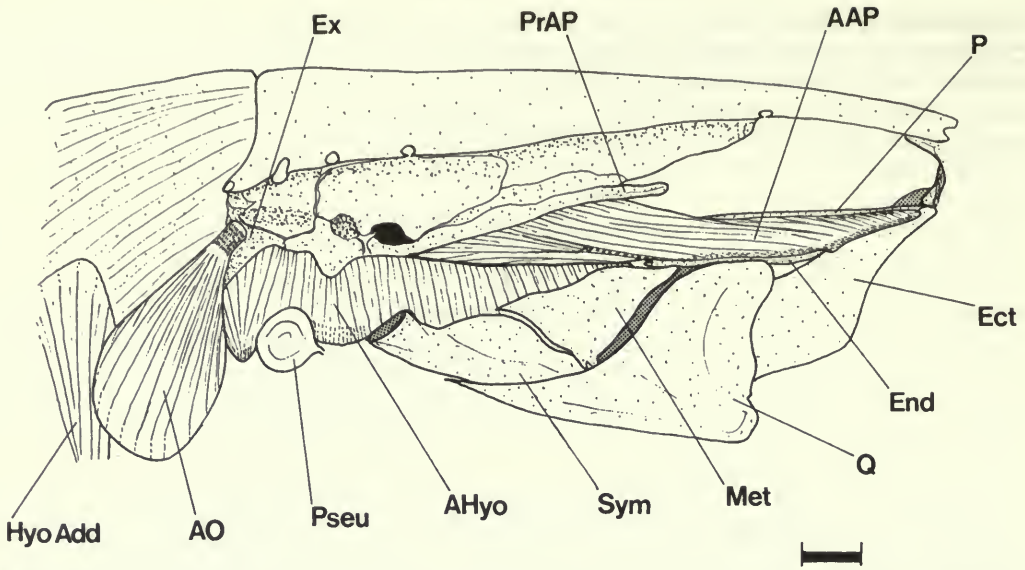


Fig. 81 *Mastacembelus mastacembelus,* deep cephalic adductor musculature after removal of the jaws, opercular series, hyomandibula and associated superficial cranial muscles; lateral view, right side.

The *adductor hyomandibulae* (Fig. 81) is well developed. Since it is apparently formed from the anterior fibres of either the *adductor operculi* or the *adductor arcus palatini* (Winterbottom, 1974), it is considered as a group two derivative.

The *adductor hyomandibulae* originates from the surface of the parasphenoid posterior to the lateral commissure. Fibres also originate from the border of the parasphenoid with the prootic in this region, and from the ventral surface of the small otic bulla in the prootic. The internal carotid foramen ventral to this bulla is covered by the *adductor hyomandibulae.* The muscle expands ventrally, and its lateral fibres insert on the ventromedial face of the hyomandibula. An anteroventral muscle slip extends below the posterior end of the *adductor arcus palatini* to insert musculously on the dorsomedial margin of the symplectic.

The *adductor arcus palatini* (Fig. 81) is an enlarged muscle extending along the side of the neurocranium from below the trigeminofacialis chamber to the lateral ethmoid. It originates mainly along the lateral face of the parasphenoid, from its anterior end (below the lateral ethmoid) to a point ventral to the lateral commissure. Fibres of the adductor also originate from the narrow lateral face of the basisphenoid and the ventrolateral face of the prootic, between the lateral commissure and the tip of its anterior process. The ventral surface of this process is trough-like, thus increasing the area available for muscle attachment.

The *adductor arcus palatini* extends between its area of origin and the dorsomedial face of the suspensorium. A series of small tendons from within the muscle merge into an aponeurosis that inserts on the posterior end of the endopterygoid. Apart from these tendons, the adductor inserts musculously on the dorsomedial face of the metapterygoid, the dorsal edge of the endopterygoid and ectopterygoid, and anteriorly, on the dorsal surface of the flattened suborbital region of the palatine.

A number of other myological features warrant description; not least of these is the distinct muscle (already noted; p. 119) originating from the posterior edge of the preoperculum and inserting on the lateral face of the operculum, ventral to the operculum ridge (Fig. 79b). The fibres of this muscle do not appear to intermingle with those of any other muscles in this region. It is innervated by a branch of the *truncus hyomandibularis* (VIIth.). Winterbottom's

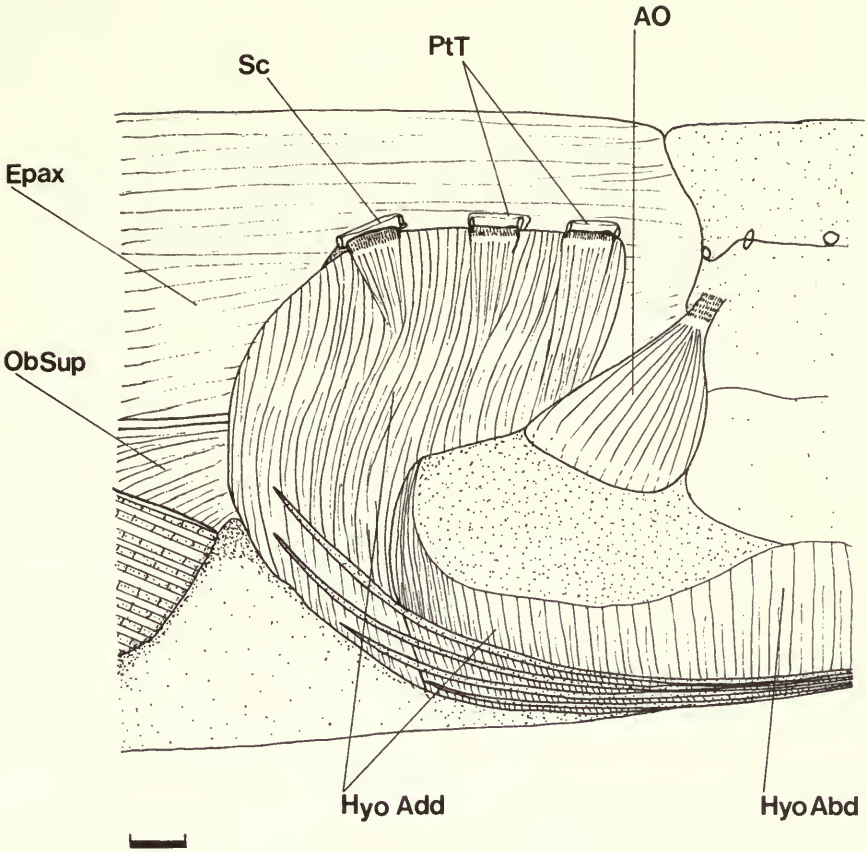


Fig. 82 *Mastacembelus mastacembelus, hyohyoidei adductores* muscle after removal of the opercular series; lateral view, right side.

(1974) synonymy gives no clue to the identity of this muscle. In view of its position within the opercular series I have named it the '*musculus intraoperculi*'. The presence of this muscle (possibly derived from the *hyohyoidei adductores;* see Travers, 1984) may be correlated with the restricted opercular opening in *M. mastacembelus,* and thus the need for an atypical method of expanding the branchial chamber.

The *hyohyoidei adductores* (Fig. 82) are large in *M. mastacembelus.* This muscle is innervated by the *ramus hyoideus* (part of the *truncus hyomandibularis* of VII), and lies anteriorly as a sheet of fibres between the distal parts of the branchiostegal rays. From there it extends dorsally above the last branchiostegal ray and continues around the dorsal margin of the operculum. The operculum partly overlies this dorsolateral expansion of the *hyohyoidei adductores,* whose lateral fibres are loosely connected to the medial face of the bone by a thin fascia. The dorsomedial face of the *hyohyoidei adductores* (above the operculum) inserts musculously along the lateral *epaxialis* musculature. The anterior edge of the muscle borders the *adductor operculi,* and there is some intermingling of their fibres. Posteriorly, the *hyoidei* inserts along the dorsolateral face of the cleithrum, the lateral face of the supracleithrum and the ventral margin of the posttemporal tubules (Fig. 82). The insertion of the muscle along the postcranial sensory canal marks its upper edge. This dorsal encroachment of the *hyohyoidei adductores* is responsible for the restricted opercular opening in *M. mastacembelus.*

The hypaxial musculature is considered to be composed of the dorsal *obliquus superioris* and the ventral *obliquus inferioris* by Winterbottom (1974).

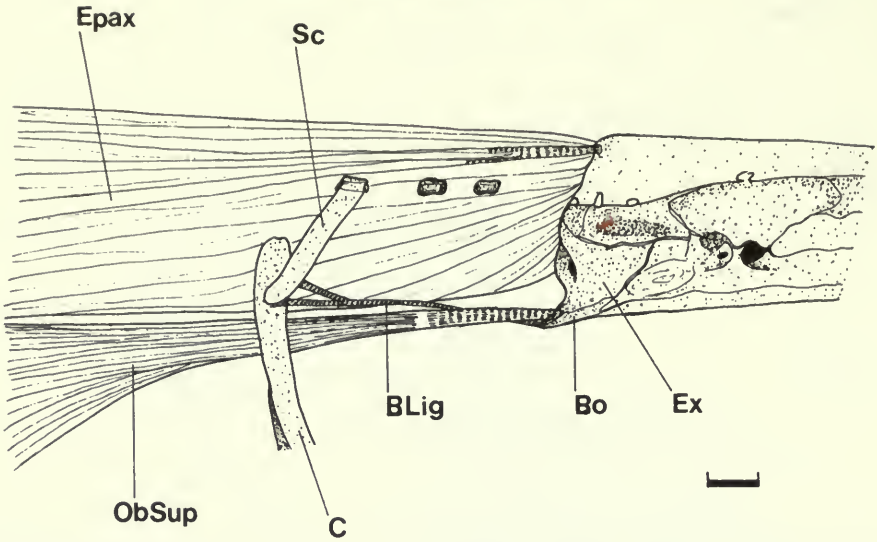


Fig. 83 *Mastacembelus mastacembelus,* epaxial musculature insertion on the basicranium and position of Baudelot's ligament; lateral aspect, right side.

The *obliquus superioris* (Fig. 83) has a particularly prominent point of insertion on the basicranium. The muscle tapers anteriorly from its posterior position along the ventrolateral wall of the body, the fibres merging into a strong aponeurosis adjacent to the medial face of the cleithrum. The aponeurosis passes along the ventral surface of the epaxial musculature, but is separated from it by the fascia covering the muscles. Anteriorly, the aponeurosis narrows into a strong tendon that inserts on the posteroventral base of the exoccipital, above its ventral border with the basioccipital.

Baudelot's ligament is small (Fig. 83), is closely associated with the prominent anterior tendon of the *obliquus superioris,* and is discernible only after careful dissection. It crosses the dorsal surface of the obliquus between its anterior connection to the basioccipital and its posterior connection to the pectoral girdle. The ligament attaches anteriorly to a shallow fossa on the posterior edge of the basioccipital, medial to the large obliquus tendon. A dense mass of adipose connective tissue in this region of the basicranium connects Baudelot's ligament to the *obliquus superioris* tendon. From its connection to the basioccipital the ligament runs posteriorly across the obliquus tendon and, anterior to the pectoral girdle, divides into an upper arm attaching to the ventromedial face of the supracleithrum, and a lower arm attaching to the dorsolateral face of the cleithrum.

Comparative myology of the Mastacembeloidei

Group one and two cephalic muscles in the majority of Asian and African mastacembeloids were examined and compared with those in *M. mastacembelus.* Unfortunately, this comparison only includes the most superficial muscles in specimens of *Chaudhuria* and *Pillaia,* partly because of their small adult size and partly because none could be serially sectioned.

Cephalic muscles

Group one muscles

The position and size of the maxillo-mandibular ligament in *M. mastacembelus* (Fig. 79a) is typical of that in the majority of mastacembeloids, including *Chaudhuria* and *Pillaia.* However, in two Tanganyikan species (*Mastacembelus albomaculatus* and *M. micropectus* Fig. 84a) and three from the lower Zairean rapids (*Mastacembelus brichardi,* Fig. 84b, *M.*

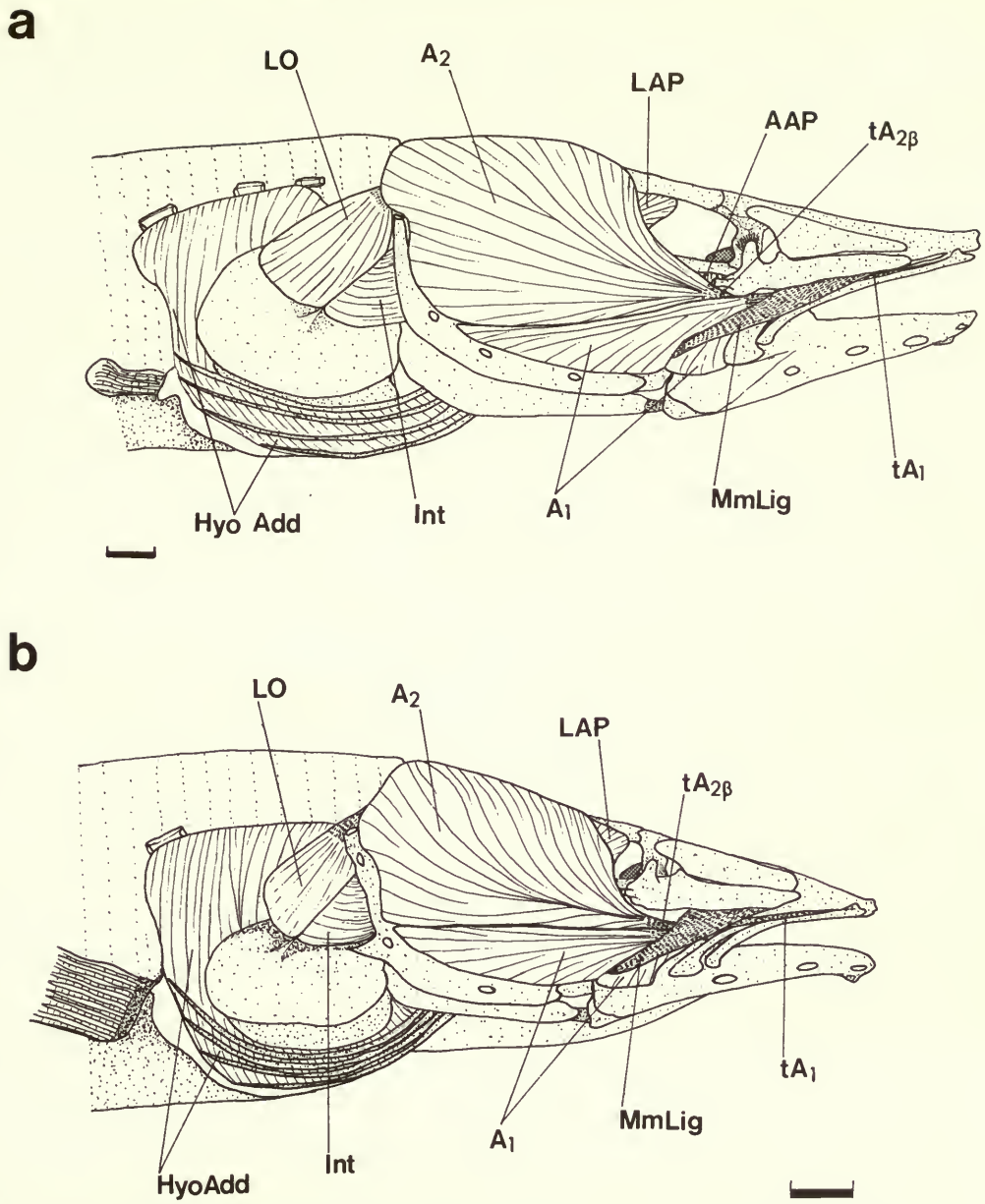


Fig. 84 Lateral view of the right superficial cephalic muscles, tendons and ligament after removal of the skin and eyeball, in (a) *Mastacembelus micropectus* and (b) *Mastacembelus brichardi*.

crassus and *M. aviceps*) the ventral attachment of the ligament is covered by the hypertrophied superficial adductor musculature. The maxillo-mandibular ligament is relatively narrow in *Mastacembelus moorii* (Fig. 85), and only attaches to the anterior end of the 1st infraorbital bone. The ligament is absent in *Mastacembelus sinensis, M. zebrinus, M. pancalus* and all *Macrognathus* species (Fig. 86a–c).

Interspecific variation in the morphology of the *adductores mandibulae* and their associated tendons is particularly noticeable in the superficial parts of that muscle complex.

The ventral position of A_1 is a diagnostic feature of all mastacembeloids. It is smaller than

A_2 in most taxa although some Asian species are exceptional. In the *Macrognathus* species (Fig. 86a), *Mastacembelus pancalus* (Fig. 86b) and *M. zebrinus* (Fig. 86c) A_1 is the largest element of the adductor complex. In these taxa it extends dorsally over the ventrolateral face of A_2, the upper edge lying on a level with the centre of the eye, and the large size of A_1 may be associated with the lack of the maxillo-mandibular ligament. Also, in these species the lateral fibres converge onto a sheet-like aponeurosis which is consolidated into a particularly long strap-like tA_1 tendon.

Part A_1 is also relatively large in a number of Tanganyikan and Zairean species (but does not exceed A_2 in size), and is a reflection of the generally hypertrophied adductor musculature in these species (see below).

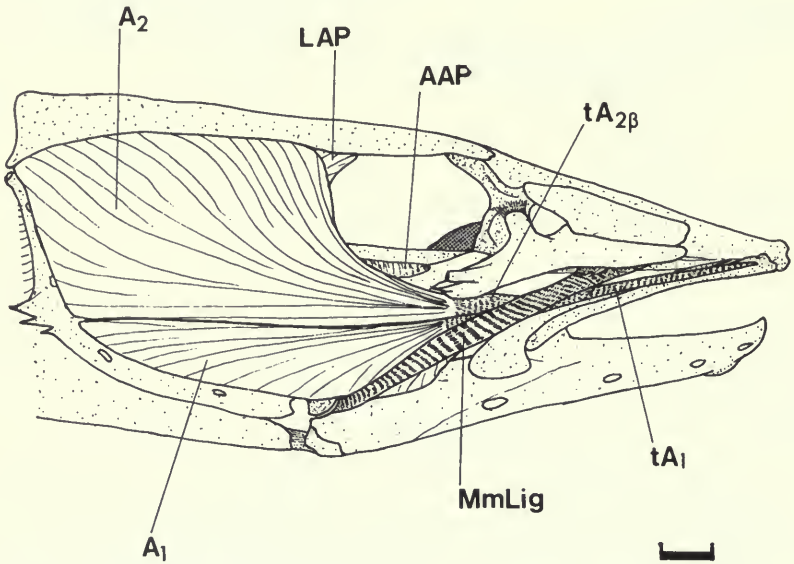


Fig. 85 *Mastacembelus moorii,* superficial *adductor mandibulae* muscle, tendons and associated ligament after removal of the skin and eyeball; lateral aspect, right side.

The inner slip of muscle originating from the anteromedial face of A_1 inserts musculously on the lateral face of the anterior tendinous part of A_2 in all mastacembeloid taxa. A_1 is small in *Mastacembelus moorii* (a Lake Tanganyikan species; Fig. 85), and has a restricted origin from the ventrolateral face of the quadrate, the anteroventral face of the preoperculum, and from the anguloarticular. In this species A_2 is large and originates from the lateral face of the symplectic and most of the preoperculum and quadrate.

The dorsolateral position of A_2 and its subdivision into two subsections ($A_{2\alpha}$ and $A_{2\beta}$) inserting tendinously on, respectively, the coronoid process and posterior tendon of A_w, are characteristic features of the superficial adductor musculature in all Asian and African mastacembeloids.

A_2 is exceptionally small in *Macrognathus* species, *Mastacembelus pancalus* and *M. zebrinus* (Fig. 86a–c), a feature combined with the enlarged A_1 in these taxa, and which may be correlated with the size and shape of the coronoid process (Travers, 1984). The posterodorsal fibres of A_2 in these taxa barely cover the *levator arcus palatini.* The fibres merge ventrorostrally and extend below the orbit, grading into a long strap-like tendon (tA_2). This tendon divides anteriorly, the small medial subsection ($tA_{2\alpha}$) inserting on the posterior aponeurosis of A_w, the larger lateral subsection ($tA_{2\beta}$) inserting on the lateral face of the broad, low coronoid process and on the dorsolateral face of the dentary.

The dorsal fibres of A_2 originate above the upper edge of the *levator arcus palatini* and part A_3, in the two Tanganyikan species *Mastacembelus moorii* and *M. ophidium.* The dorsal surface of the skull in these species is relatively narrow, and the expanded A_2 fibres originate from its dorsolateral margin.

The adductor muscles, particularly A_2, are hypertrophied to an unparalleled extent in the microphthalmic and cryptophthalmic mastacembeloids. *Pillaia* (from Asia; Fig. 87), *Mastacembelus micropectus* and *M. albomaculatus* (Lake Tanganyika; Fig. 84a) and *M. brachyrhinus, M. brichardi, M. crassus, M. aviceps* and probably *M. latens* (from the lower Zairean rapids; Fig. 84b).

The adductor musculature in *Mastacembelus brichardi* was described by Poll (1973). This species is markedly cryptophthalmic and its reduced eyes lie below A_2 and the *levator arcus palatini.*

In all the cryptophthalmic and microphthalmic taxa the roof of the skull slopes ventrally and the massive A_2 originates from the dorsal surface of the frontal postorbitally, and from the entire dorsal surface of the parietal. The dorsomedial face of each A_2 contacts its partner in the midline (their fibres not interconnecting) in all but *Pillaia* and *M. brachyrhinus,* in these species A_2 is not hypertrophied to such an extreme extent as it is in the others.

Part A_3 of the *adductor mandibulae* lies medial to the *levator arcus palatini* and has a similar origin and insertion in all mastacembeloids (p. 118). The size of the coronomeckelian is an indication of the size and strength of the A_3 muscle and its anterior tendon (tA_3). The extent to which the tendon of A_3 ossifies varies widely among the Asian and African taxa, (see above p. 80).

Part A_w shows no marked departure from the condition described for *M. mastacembelus* (p. 119).

In all species the *levator arcus palatini* lies between divisions A_2 and A_3 of the *adductor mandibulae*; it originates from the dorsolateral edge of the neurocranium and inserts musculously along the dorsolateral face of the suspensorium. The levator fibres merge ventrally into a wide, transparent, sheet-like aponeurosis which is particularly thin in a number of Asian (e.g. *Mastacembelus sinensis* and *M. armatus*) and African species (e.g. *M. frenatus, M. moorii* and *M. batesii*). This condition of the levator appears to have a mosaic distribution among the mastacembeloids. The posterodorsal fibres intermingle with those from the anterior margin of the *dilatator operculi* in all taxa.

The ventral apex of the *dilatator operculi* inserts tendinously on the dorsal surface of the opercular dilatator process in all mastacembeloids.

The extent to which the lateral face of the dilatator is covered by the preoperculum and the A_2 division of the *adductor mandibulae* depends on the degree to which the latter are developed. In those species with a protracted vertical arm of the preoperculum, for example *M. longicauda* and *M. reticulatus*, the lateral face of the dilatator is completely covered, as it is in those species with a particularly massive A_2 muscle (p. 87 & Fig. 84).

Group two muscles

The *levator operculi* shows little interspecific variation apart from slight differences in relative size. The muscle insertion on the dorsolateral face of the operculum, is a characteristic feature of all mastacembeloids. A large levator, (relative to its size in *M. mastacembelus*) occurs in *M. albomaculatus*; its ventrolateral fibres traverse the low opercular ridge in this species, and intermix with the dorsolateral fibres of the *'intraoperculi'* muscle.

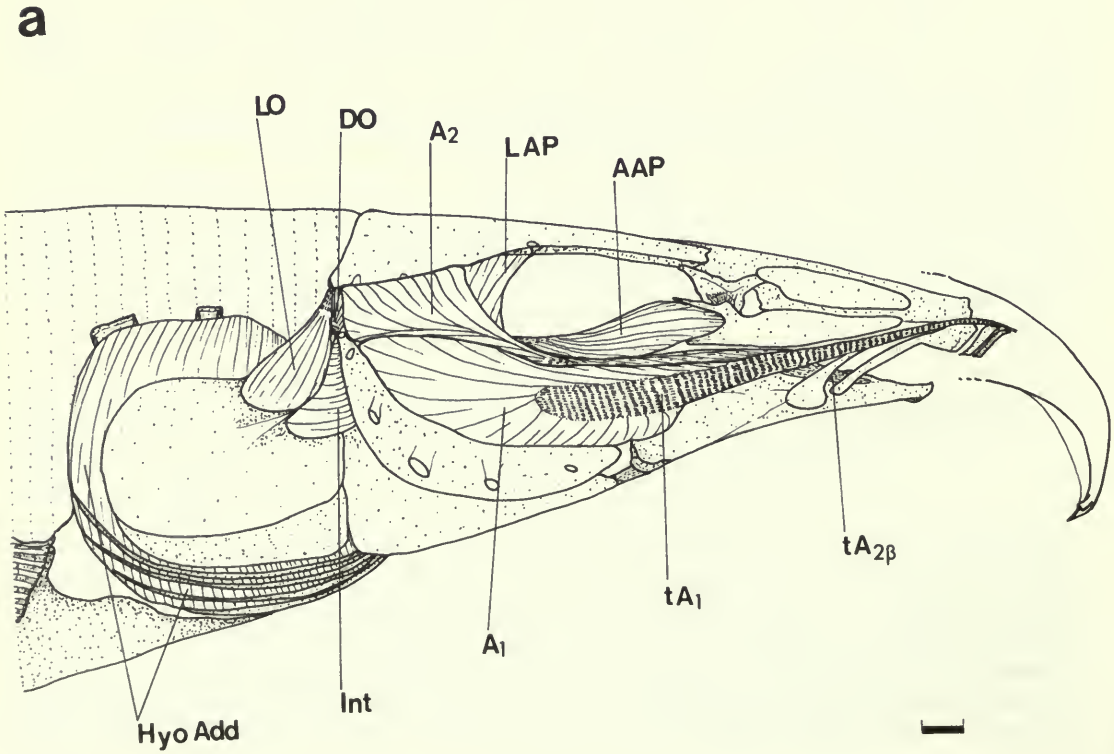
The morphology of the *adductor operculi* also shows little interspecific variation. The fibres along the posterior margin of the muscle intermingle, in all species, with the dorsolateral part of the *hyohyoidei adductores* in a manner similar to that described in *M. mastacembelus* (p. 119). The pseudobranch lies between the posteromedial margin of the *adductor operculi* and anteromedial face of the *adductor hyomandibulae* in all the species investigated.

There is little interspecific deviation of the *adductor hyomandibulae*; it is particularly well-developed in all mastacembeloids. The muscle originates from the posteroventral region of

the parasphenoid and prootic (including the ventral surface of the otic bulla), and inserts on the medial face of the symplectic and hyomandibula (Fig. 81).

The marked interspecific variation in the arrangement of the *adductor arcus palatini* muscle involves, posteriorly, its site of origin along the ventrolateral face of the braincase, and anteriorly, its connection to the enlarged 1st infraorbital bone. The anterior region of the *adductor arcus palatini,* compared with its condition in *M. mastacembelus* (Fig. 81), is modified in a number of Asian taxa including the *Macrognathus* species, *Mastacembelus pancalus, M. zebrinus, M. keithi, M. caudiocellatus* and *M. maculatus* (see Figs 86 & 88). The anterior fibres of the muscle in these taxa extend from the anterolateral face of the parasphenoid across the ectopterygoid to insert musculously along the posterior edge of the 1st infraorbital. In *M. zebrinus* (Fig. 88a) this extension is little more than the lengthening of the anterolateral fibres of the adductor which form the orbital floor. However, in *Macrognathus* (particularly *M. aculeatus;* Fig. 88b) the anterior region of the *adductor arcus palatini* is unconnected to the fibres which form the orbital floor, apart from some slight contact along the anteromedial margin. The medial end of this virtually distinct anterior muscle in *Macrognathus aculeatus* is connected, tendinously, to the anterior end of the parasphenoid along its dorsolateral margin. The muscle fibres extend anterolaterally around the edge of the orbital cavity, crossing but not connecting to the anterodorsal face of the ectopterygoid. The anterior end of the fibres in this region merge into a broad aponeurosis which inserts on the attenuated posterior edge of the 1st infraorbital (Fig. 41a).

This anterior differentiation of the *adductor arcus palatini* may be correlated with the large rostral appendage in the species involved. The uniquely trunk-like rostral appendage in *Macrognathus,* where the muscle is found in its most highly developed form, lends support to this view. Contraction of the anterior adductor would result in movement of the large 1st infraorbital bone which contributes to the complex musculo-skeletal system that governs the movement of the highly mobile rostral appendage in these taxa.



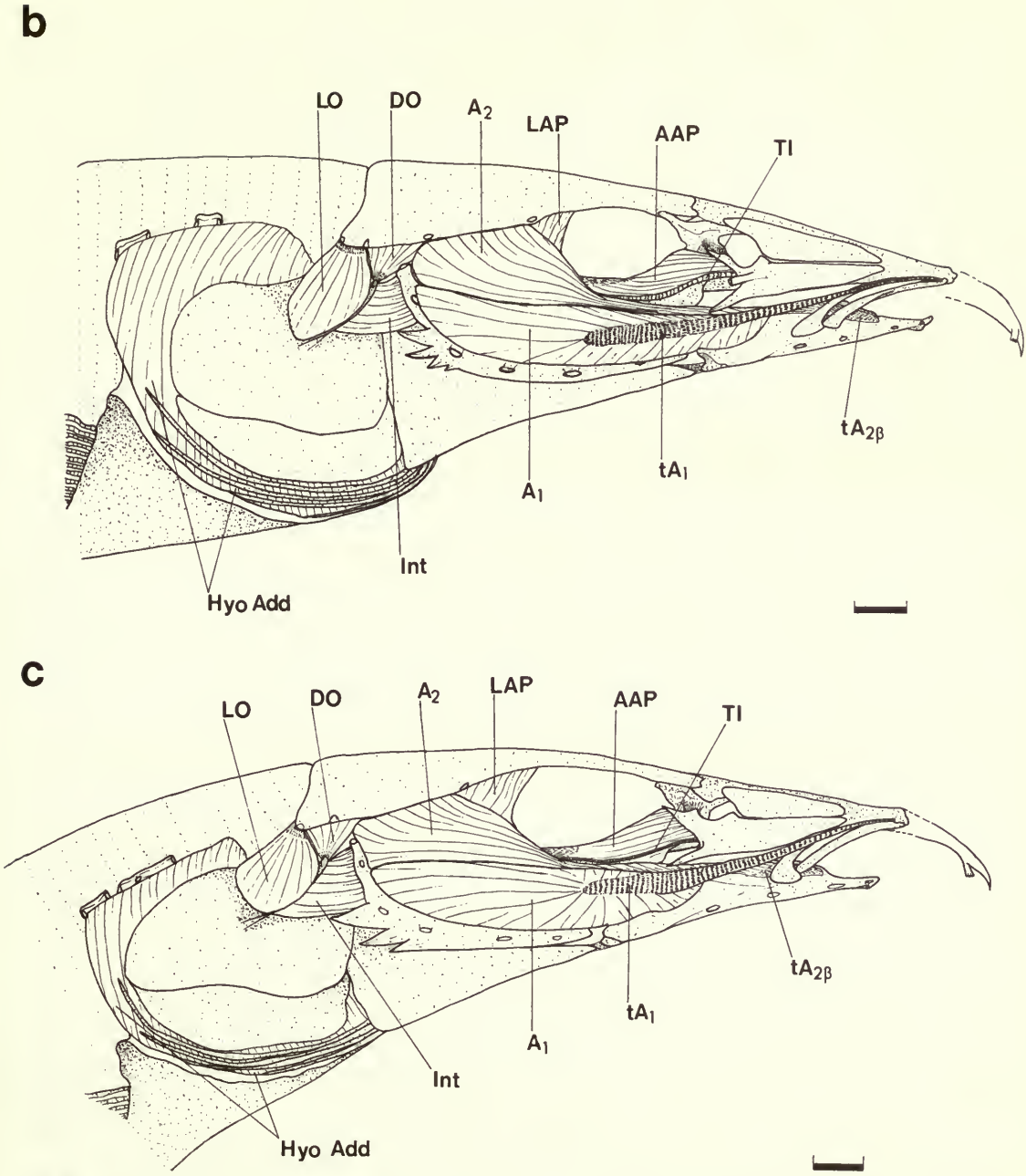


Fig. 86 Lateral view of the right superficial cephalic muscles, after removal of the skin and eyeball, in (a) *Macrognathus aculeatus,* (b) *Mastacembelus pancalus* and (c) *Mastacembelus zebrinus.*

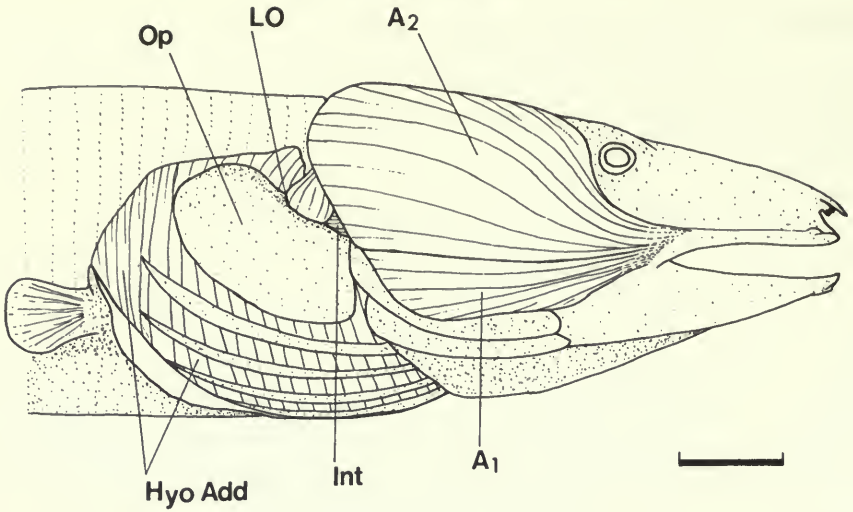


Fig. 87 *Pillaia indica,* superficial cephalic muscles after removal of the skin; lateral view, right side.

The anterior fibres of the *adductor arcus palatini* do not insert on the posterodorsal surface of the palatine in *Mastacembelus armatus* or *Mastacembelus erythrotaenia* and hence do not form the orbital floor in these species.

The *adductor arcus palatini* originates posteriorly, in the majority of mastacembeloids, along the ventrolateral face of the prootic and ventral surface of its anterior process (as described in *M. mastacembelus* p. 120). The lack of a long anterior prootic process in some species results in a smaller area available for the origin of the adductor. The absence of this process may be associated with the presence of only a relatively small rostral appendage and the lack of an enlarged anterior region of the adductor in these species (e.g. *Mastacembelus tanganicae* p. 61).

The need to provide an increased area of origin for the long *adductor arcus palatini* is probably a further factor influencing the development of the anterior process on the prootic generally found in mastacembeloids.

Of the other myological features; the *'musculus intraoperculi'* (p. 121) is a unique characteristic of all mastacembeloids. In the majority of taxa its fibres are unconnected to those of any other cephalic muscle (Figs 79a & 84–87).

The *hyohyoidei adductores* shows little interspecific variation in their arrangement. The dorsolateral expansion of the muscle, and its musculous insertion on the cleithrum, supracleithrum and posttemporal tubules are features common to all taxa, including *Chaudhuria* and *Pillaia.* This branchiostegal muscle is responsible for restricting the opercular opening since it extends over, and is inserted on, the ventrolateral face of the epaxialis musculature.

The *obliquus superioris* is similar in all mastacembeloids, and its anterior tendinous insertion on the posteroventral face of the exoccipital is a characteristic feature of the group. The wide anterior tendon inserts laterally in a shallow basioccipital fossa medial to which the basioccipital accommodates the anterior end of Baudelot's ligament.

A small, relatively weak Baudelot's ligament, as described in *M. mastacembelus* (p. 122), is present in all taxa. It is closely connected to the large anterior obliquus tendon ventrally, and with the ventral surface of the epaxialis musculature dorsally. In most species the ligament crosses the dorsal surface of the obliquus tendon before attaching to the pectoral girdle. However, in *Mastacembelus longicauda* it crosses ventrally, below the tendon. A divided posterior end of Baudelot's ligament, inserting on both the cleithrum and the supracleithrum, is also a feature common to all mastacembeloids.

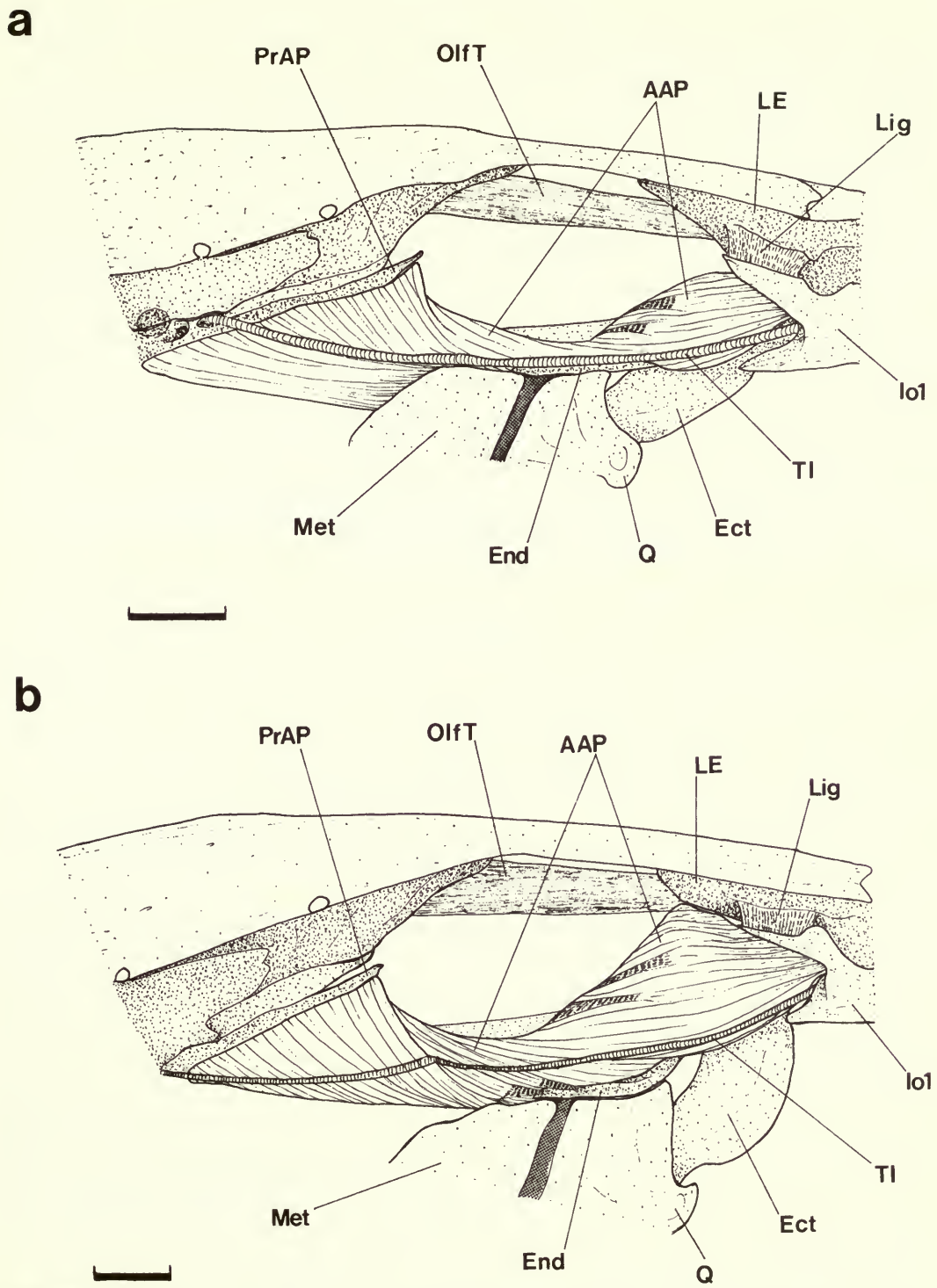


Fig. 88 Lateral view of the right *adductor arcus palatini* muscle in (a) *Mastacembelus zebrinus,* and (b) *Macrognathus aculeatus.*

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Dr Ethelwynn Trewavas

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Synopsis

The spider subfamily Spartaeinae nom. n., is defined; a key to genera and species check list are provided. Morphological characters and generic affinities both fossil and recent are discussed. Six new genera, *Meleon, Mintonia, Neobrettus, Taraxella, Veissella* and *Yaginumanis* are proposed. *Spartaeus* Thorell and *Gelotia* Thorell are revised. Distributional data are given and separate keys to the species of *Gelotia* and *Mintonia* are provided. The genera *Cocalus* Koch, *Cyrba* Simon, *Phaeacius* Simon, *Portia* Karsch and *Veissella* are illustrated by figures of selected species. All the known species of *Gelotia, Mintonia, Neobrettus, Spartaeus, Taraxella, Yaginumanis,* the newly discovered males of *Brettus anchorum* Wanless and *Meleon solitaria* (Lessert) are figured and described. The type material of 12 nominate species was examined and seven lectotypes designated. One generic and three specific names are synonymised, and seven new combinations are proposed.

Introduction

This study completes a preliminary revision of recent salticids formerly included in the subfamily Boethinae. Unfortunately the nominate genus *Boethus* Thorell, 1878 is a junior homonym of *Boethus* Foerster, 1868 and a new subfamily name (Spartaeinae) must be proposed. However, as a result of synonymy (see p. 148) the type species remains unchanged.

Simon (1901) stated that *Boethus* appeared to be transitional between *Lyssomanes* Hentz, *Cocalodes* Pocock and *Linus* Peckham & Peckham (=*Portia* Karsch) and proposed the subgroup Boetheae comprised of two genera, *Boethus* and *Portia.* Petrunkevitch (1928) subsequently reorganised the subgroup by elevating Boetheae to subfamily rank to include salticids characterised by their fairly large posterior median eyes. Roewer (1954) adopted Petrunkevitch's system, but divided the subfamily into five groups (Table 1). Of the genera listed, three, *Cocalodes* (revised Wanless, 1982), *Sonoita* Peckham & Peckham and *Holcolaetis* Simon, are removed from the Spartaeinae because the male palps possess a median apophysis (see below). The systematic position of a fourth genus *Tanna* Berland is uncertain

Table 1 List of genera in the subfamily Spartaeinae (sensu Roewer, 1954)

1. Gr. Boetheae	3. Gr. Lineae
Boethoportia Hogg	*Linus* Peckham & Peckham
Boethus Thorell	*Tanna* Berland
Portia Karsch	4. Gr. Cocalodeae
2. Gr. Cocaleae	*Cocalodes* Pocock
Cocalus Koch	*Sonoita* Peckham & Peckham
Phaeacius Simon	5. Gr. Holcolaeteae
	Holcolaetis Simon

Table 2 Revised list of genera in the subfamily Spartaeinae

RECENT	
Brettus Thorell	*Neobrettus* gen. n.
Cocalus Koch	*Phaeacius* Simon
Cyrba Simon	*Portia* Karsch
Gelotia Thorell	*Spartaeus* Thorell
Meleon gen. n.	*Taraxella* gen. n.
Mintonia gen. n.	*Veissella* gen. n.
	Yaginumanis gen. n.
FOSSIL	
Almolinus Petrunkevitch	*Eolinus* Petrunkevitch
Cenattus Petrunkevitch	*Paralinus* Petrunkevitch
	Prolinus Petrunkevitch

as the male palpal organs are of a relatively simple euophryine type and show no affinities with other genera listed in the subfamily.

The Spartaeinae, as defined here, is now comprised of 13 recent and five fossil genera (Table 2). Of the recent genera, four have been revised—*Brettus* Thorell, *Cocalus* Koch, *Phaeacius* Simon and *Portia* (see Wanless, 1978*b*, 1979, 1981*a*, 1981*b*), and a paper on *Cyrba* Simon, is in preparation. Two genera are here formally transferred into the Spartaeinae from other subfamilies; *Cyrba* from the Plexippinae (sensu Prószyński, 1976) and *Gelotia* Thorell from the Magoninae. One genus, *Portia*, has been relimited and six new genera are proposed. The introduction of so many new genera in a family which is almost certainly overloaded with generic synonyms requires some explanation. Firstly, with the partial exception of *Cyrba*, all of the taxa thought to belong in this subfamily have been examined. Secondly, the subfamily is distinctive and would have been intuitively recognised by early taxonomists from the presence of relatively large posterior median eyes. Although it is now considered that at least two subfamilies are involved, the species concerned would even under Simon's classical system have been placed systematically close to one another. Exceptions may occur amongst those genera in which the posterior median eyes have been reduced, as for example in *Cyrba* and some species of *Gelotia*. Finally an attempt has been made to limit genera on the basis of synapomorphies and then place them in small and hopefully recognisable monophyletic groups, precisely the strategy advocated by Platnick & Shadab (1979).

The standard abbreviations and measurements are those used by Wanless (1978*a*), but for the leg spination the system adopted is that used by Platnick and Shadab (1975).

Morphological characters

The following account of selected morphological characters provides the basis for the present taxonomic conclusions and clarifies some points which have been misinterpreted in earlier revisions (Wanless, 1978*a* & *b*). One new character, the femoral organ, is described and simple abbreviations (M_1, M_2, M_3) used to designate elements of the distal haematodocha and palpal tegulum.

Posterior median eyes

These eyes are usually classified as being either small/minute or relatively large in relation to the posterior lateral eyes and I cannot recall a single instance in which there has been difficulty in assigning one state or the other. In the majority of salticids the posterior median eyes are small and it has been shown that in some species, *Metaphidippus harfordii* (Peckham

& Peckham) and *Phidippus johnsonii* (Peckham & Peckham), their retinae are vestigial (Eakin & Brandenburge, 1971). By contrast, in *Portia* they are large (Wanless, 1978*b*) and the retinal anatomy is non-degenerate as in the other lateral eyes (Blest, 1983; pers. comm.). It is therefore assumed that large posterior median eyes are primitive for Salticidae.

As far as I am aware, large posterior median eyes only occur in fossil genera (see Table II) and in recent old world genera of the subfamilies Lyssomaninae and Spartaeinae, and the *Cocalodes*-group of genera (i.e. *Cocalodes* Pocock, *Allococalodes* Wanless, *Holcolaetis* Simon and *Sonoita* Peckham & Peckham). They have been reduced at least four times in the Lyssomaninae, *Lyssomanes* Hentz and *Chinoscopus* Simon from the new world, *Pandisus* Simon and *Onomastus* Simon from the old, and twice in the Spartaeinae i.e. *Cyrba* and *Gelotia.* The latter genus including four species with large posterior median eyes and two with small. Homann (1971) has suggested that in spiders the eyes were originally more or less arranged in parallel rows of four equal sized eyes, that specialisation within families occurred through the enlargement of some eyes and their corresponding optic areas of the brain. Ontogeny has shown that in salticids the posterior eye row is primarily procurved and that eyes normally referred to as the posterior medians are in reality the posterior laterals. In the same work, Homann treated lyssomanine spiders as a distinct family, the Lyssomanidae, and demonstrated that their secondary eyes (i.e. AL, PM, PL), unlike those of the Salticidae, have all the retinal nuclei distal to the rhabdomes, as in most spiders, and not outside the pigment cups as in the Salticidae. Also, the lateral eyes lack elongated rods. Further studies by Blest (1983, pers. com.) confirm that the secondary eyes of *Lyssomanes* are different from those of advanced salticids. However, he advises against placing too much taxonomic weight on the importance of eye characters as they are liable to rapid selection. Clearly, the eyes of old world lyssomanines (sensu Wanless, 1980*c*) should be examined before drawing any phylogenetic conclusions. For the present therefore, I would still maintain that lyssomanine spiders merit only subfamilial rank while at the same time drawing attention to the fact that the monophyly of the group has still to be proven.

Cheliceral teeth

The structure and number of teeth on the inner margins of the chelicerae have been used to divide the Salticidae into three major divisions, the Unidentati, Fissidentati and Pluridentati (Simon, 1901). The system has been much criticised (Petrunkevitch, 1928; Prószyński, 1971*a*; Wanless, 1975; Kaston, 1981) on the grounds that it is artificial and there are numerous examples where the number and structure of the teeth are intraspecifically inconsistent or asymmetrical. It has also been argued, correctly in my view, that the fissidentate tooth i.e. a tooth with two or three points, is essentially transitional between a single tooth (unidentate) and two or more separate teeth (pluridentate). Unfortunately, and contrary to the remarks of Lehtinen (1975) and Wanless (1980*b*), the sister group of the Salticidae is far from certain, it is therefore difficult to decide if the presence of numerous teeth on the inner margin represents a primitive or derived condition. Salticids lacking teeth or with a single tooth on the inner margin tend to share more derived characters i.e. small posterior median eyes and relatively simple (?) secondarily reduced male palpal organs, suggesting that the absence of teeth may also be a derived condition. However, even if these assumptions are correct they tell us little of the phylogeny as the trend towards a reduction in the number of teeth has probably occurred on numerous occasions.

While there can be no doubt that the divisions are artificial, it is suggested that contrary to current opinion we may yet find that they form useful key characters. For in practice the vast majority of salticids can be easily sorted into one division or another. Exceptions will of course always occur, but once recognised they may be allowed for in the key.

Fovea

The fovea can sometimes provide a useful key character, but it does not appear to be of much use in assessing relationships as its length and position are variable and seemingly

unrelated to carapace shape. In species of both Lyssomaninae and Spartaeinae the fovea is generally elongate, and positioned further back on the thorax than is usual in many other groups, suggesting that it may represent a primitive condition. The derived state is either its absence or a more forward location—usually more or less between the posterior margins of the posterior lateral eyes.

Femoral organ (Figs 30A–F; 32A–D)

This unusual structure only occurs on the underside of the femora of the first pair of legs in some males belonging to the genera *Brettus, Gelotia, Mintonia* gen. n., and *Spartaeus.* It varies in development and has probably been lost in some species. In *Spartaeus spinimanus* (Thorell) and *Gelotia bimaculata* Thorell, the femoral organ is represented by a small angular tubercle bearing a shallow perforated depression surrounded by irregular pleats (Fig. 30A–F). It is clearly visible under the optical microscope, but in species where the tubercle is lacking the organ may be recognised as a pale amber spot or streak. In *Mintonia tauricornis* sp. n., the femoral organ, appearing as a pale amber spot under low power, is probably non-functional consisting of a ring of pleats with the central perforations lacking (Fig. 31A). *Mintonia ramipalpis* (Thorell) is similar, but there are scattered pores a few of which are apparently setose (Fig. 31B–D). However, in an untreated specimen, i.e. one which had not been cleaned in an ultrasonic bath previous to coating for SEM, the femoral organ is seen to contain numerous amorphous globules, almost certainly a secretion (Fig. 31E–F). Some globules are still attached to the secretory pores a few of which are evidently plugged (Fig. 31F, arrowed), but in reality the beginning of an exudate; it therefore seems unlikely that 'true' setose pores are present. The phenomenon is in one sense an artifact as the exudate, possibly a sex pheromone, will have been produced and coagulated while the specimen was languishing in spirit. In *Brettus cingulatus* Thorell, the femoral organ, appearing as a minute pale amber streak and overlooked by Wanless (1979), has the form of a perforated gully which appears to contain an amorphous secretion (Fig. 32A–C).

When poorly developed and only evident as a pale amber spot, the femoral organ resembles those sometimes found on the first and second pairs of legs of certain female spiders in the family Mysmenidae (Platnick & Shadab, 1978). Unfortunately mysmenids are rare in collections and it has only been possible to examine the legs of a single unidentified Portuguese species. The first sample, a leg I, disintegrated in preparation and was lost; the second, a leg II, shows the femoral organ as a rather featureless spot (Fig. 32D) which bears a passing resemblance to that found in *M. tauricornis* (Fig. 31A). In some mysmenids, including the Portuguese species, the femoral organ appears to be more pronounced on the first pair of legs, while some published figures suggest that the organ has the form of a low mound (Kraus, 1967; Brignoli, 1980). Clearly further studies are warranted, but as salticids and mysmenids belong to different phyletic groups it would be surprising if the femoral organs proved to be homologous.

For the present, well developed femoral organs are regarded as primitive, the derived condition being their vestigial state or absence. On the whole they have been of little use in resolving intergeneric relationships.

Retrolateral tibial apophysis (RTA)

The retrolateral tibial apophysis shows a degree of development which is evidently unparalleled within the Araneae. In some genera e.g. *Portia, Phaeacius* and *Yaginumanis* gen. n., it is a solid, occasionally ramose prong (Figs 6E; 28A; 29D), while in others it has associated ducts with median or distal openings (Figs 21D; 32E, F; 33A–F). In one genus, *Cocalus,* the RTA is saucer-shaped and supports a membraneous finger-like extension of the tibia (Fig. 22C). Yet other genera (*Cyrba, Gelotia* and *Meleon* gen. n.) are characterised by RTAs which arise from a membraneous base, some of which may be moveable (Figs 20C; 26F).

In *Gelotia syringopalpis* sp. n., and *Mintonia melinauensis* sp. n., the openings of the apophyses can be seen under the optical microscope (Figs 21D; 13C), but in other species

the openings can only be detected by SEM (Figs 32E, F; 33A–E). Unfortunately it has only been possible to examine a few specimens and experience has shown that it is probably unwise to assume the presence of openings. For example, the RTA of *Mintonia ramipalpis* (Thorell) has every appearance of possessing a duct, but this was not confirmed by SEM studies (Figs 14H; 34A, B). Also, the occurrence of a membraneous base to the RTA is not necessarily indicative of openings—compare *G. bimaculata* Thorell which has an opening (Fig. 33A, B) with *Meleon kenti* (Lessert) and *Cyrba algerina* (Lucas) in which they are lacking (Fig. 34C, D, F).

The purpose of these complex apophyses is unknown. They could be functionally homologous with the femoral apophyses of *Asemonea* O.P.-Cambridge and *Pandisus* Simon (see Wanless, 1980*c*) and produce a contact pheromone or secretion for plugging the female copulatory openings. In *G. bimaculata* there is a sclerotised fold opposite the posterior margin of the epigyne (Fig. 17C, arrowed) suggesting that this region may receive the tip of the RTA. However, there is no evidence to indicate that this may occur in other species or genera. The apophysal openings may have been lost in some species of *Mintonia* and it is possible that ducted apophyses are a primitive, rather than an advanced character in salticids.

Distal haematodocha

Wanless (1978*b*) referred to the distal haematodocha of *Portia* as a tripartite membraneous apophysis. This was incorrect since fresh material has shown that although the three elements are contiguous only two, for convenience labelled M_1 and M_2, can properly be described as being part of the distal haematodocha. The third element discussed below and labelled M_3 is thought to represent a separate distal modification of the tegulum.

In ventral aspect M_1 lies partially over the embolic base and is usually on the prolateral side of the embolic duct where it enters the embolus. It often develops a minute lobe (Fig. 16A–C), but in *Neobrettus* and *Cyrba* they are large and petal-like (Figs 24D; 25F), while in *Phaeacius* there is a long filamentous process, erroneously labelled as a secondary conductor in Wanless (1981*a*). M_2 lies on the retrolateral side of the embolus and is often seen as a small lobe or membraneous patch lying alongside or slightly apart from the embolus (Fig. 16A–C). Only occasionally does it extend posteriorly to produce a translucent ledge, *Brettus,* or fuse with M_3, *Gelotia.* In ventral aspect M_3 lies above M_2 and usually extends transversely or obliquely across the tegulum forming a narrow, delicate translucent ledge in *Portia* and *Meleon,* a lobe in many species of *Mintonia* and a short filament in *Spartaeus.* In *Gelotia* it takes the form of a curtain-like membrane not readily separated from M_2.

Although the distal haematodocha and tegular ledge are sometimes characteristic of spartaeine genera, the development of the former in other salticids is uncertain as it is not always evident in unexpanded palps, possibly being overlooked, whereas the tegular ledge seems to have no parallel in other salticids. The complexity of the distal haematodocha and presence of a tegular ledge may in themselves be synapomorphic for Spartaeinae.

Tegular furrow

This structure which forms an integral part of the tegulum varies considerably. It is sometimes obscured by the embolus, distal haematodocha and the tegulum itself, especially when bulbous. It is usually situated on the retrolateral side of the tegulum and may be recognised as a pit, which is sometimes dark and may extend posteriorly as a groove alongside the retrolateral margin. Below the cuticle of the tegulum, adjacent to the pit or near the base of (M_3) there is sometimes a black disc-like structure (Fig. 19F). The pit may be shallow and open with a thick anterior wall and slight hood (Fig. 24D), deep and almost circular (Fig. 35C), irregular or crescent-shaped (Fig. 9C). The groove may be deep (Fig. 36E), lacking or short and shallow (Figs 12E; 35E), occasionally terminating in a series of fine striae (Fig. 22D). In at least two species, *Phaeacius lancearius* (Thorell) (see Wanless, 1981*a*) and *Brettus cingulatus* Thorell, there is a minute pore in the wall of the pit which is evidently lacking in other genera.

The furrow is not known to occur in other Salticidae and its presence is regarded as a synapomorphy linking all members of this subfamily. Its function is unknown.

Ventral tibial apophysis

The ventral tibial apophysis often has a characteristic oblique profile (Figs 7G; 19F; 22D) when viewed in ventral aspect. It varies in development and is usually obscured by tibial setae in the intact unshaven palp. It was initially considered to represent a second synapomorphy supporting this subfamily, but the occurrence of a similar apophysis in certain amber salticids (p. 146, Fig. 2A) believed to share closer affinities with the *Cocalodes*-group of genera raises doubts as to the validity of the proposal.

Cymbium

The basal region of the cymbium is often modified. In some genera e.g. *Portia, Cyrba* and *Gelotia* there are evidently non-functional protuberances and excavations, while in others there are dorsal protuberances and recesses that interlock with tubercles on the palpal tibiae, which would appear to limit the extent to which the cymbial/tibial joint can be articulated. A similar protuberance on the palpal patella limits the flexing movement of the tibia. Provisional observations suggest that in *Cyrba* and *Meleon* the development of the locking mechanism is variable. In *Mintonia, Phaeacius, Spartaeus Taraxella, Veissella* and *Yaginumana* it is lacking or poorly developed, while in *Brettus, Gelotia, Neobrettus* and *Portia* it is relatively strong. Also, in *Brettus* and *Neobrettus* there is a basal retrolateral excavation which is apparently used, at least in part, to protect the tip of the long filamentous embolus (Figs 23F; 24C). The floor of the excavation is membraneous and seems to be contiguous with the segmental membrane uniting the cymbium and tibiae. A similar, rather subtriangular region is found in some species of *Meleon* (arrowed Fig. 26B). Its purpose is unknown, but in *Meleon,* at least the membraneous area plays no part in retaining the embolus.

Although some cymbial modifications are unique to the genera concerned, the locking mechanism is probably a primitive feature of these palps, and in any event, as a character it has not been of much use in determining affinities.

Median apophysis

This male palpal structure, which does not occur in members of this subfamily, is only found in Lyssomaninae, the *Cocalodes*-group of genera (see p. 138) and the amber genus *Eolinus.* Within these groups it is sometimes seen as a (?) moveable bifid prong which arises from a membraneous or pleated region of the tegulum (Fig. 1A; see also Wanless, 1982). Its occurrence in *Eolinus* and the implications thereof are discussed below.

Subfamily ***SPARTAEINAE*** nom. n.

Boetheae Simon, 1901: 388, 400.
Boethinae Petrunkevitch, 1928: 57, 181; 1939: 184. Bonnet, 1955: 892. Roewer, 1957: 933.

REMARKS. In spite of Bonnet's remarks (Bonnet, 1955), Strand (1929) was correct to regard *Boethus* Thorell, 1878 as a junior homonym of *Boethus* Foerster, 1868. However, his replacement name (*Boethuola*) cannot be justified as *Spartaeus* Simon, a junior synonym of *Boethus,* is available. Since the subfamily name Boethinae is therefore invalid it is proposed that *Spartaeus* becomes the nominate genus of the subfamily Spartaeinae. In reality only the nomenclature has changed as the type species of *Spartaeus* (*S. gracilis* Thorell) is a junior subjective synonym of *Boethus spinimanus* Thorell, the type species of *Boethus.*

DEFINITION. A heterogeneous group of spiders ranging from about 3·0 to 11·0 mm in length. Markings occasionally conspicuous; general habitus sometimes hirsute with tufts and fringes. *Carapace*: of various shapes, usually elevated with highest point at about level of posterior

lateral eyes, rarely near centre of thoracic part; fovea usually long, sulciform and situated more or less just behind posterior lateral eyes. *Eyes*: in three rows, those of the second often fairly large. *Clypeus*: low to high with three long setae in lower space between anterior median eyes. *Chelicerae*: moderately robust, usually stronger in female; vertical or slightly inclined anteriorly, more or less parallel or slightly diverging; apophyses or spurs lacking; promargin with three to seven teeth, retromargin with three to nine, variously described as teeth or denticles. *Maxillae*: moderately long to long with outer distal margins varying from rounded to oblique; modifications lacking. *Labium*: about as long as broad or longer than broad. *Sternum*: more or less elongate scutiform. *Abdomen*: usually elongate ovoid with four indistinct apodemal spots; markings variable; spinnerets moderately long; anal tubercle cone-like; position of colulus usually indicated by scanty tuft of setae between tracheal spiracle and base of anterior spinnerets; tracheal spiracle an obscure transverse slit near base of anterior spinnerets. *Legs*: usually long and slender with numerous spines; sometimes strongly fringed; claws usually pectinate; tufts present; scopulae absent, but minute iridescent setae often present on tarsi and metatarsi; some males with femoral organs on first pair of legs (Figs 30A–F; 31A–F). *Female palps*: generally moderately long and slender with apical claw. *Male palps*: generally complex, sometimes with interlocking tubercles between cymbium/tibia and tibia/patella; tibiae with somewhat oblique ventral apophyses, rarely reduced, and usually complex retrolateral, rarely dorsal, apophyses sometimes possessing membraneous elements, distal openings or adjacent tube-like process; cymbium with distal scopula, often with basal protuberances or excavations; embolus usually slender, of various lengths, arising apically or from prolateral side of tegulum, pars pendula or basal sheath rarely evident; distal haematodocha usually bearing delicate transparent or translucent lobes, flanges or filaments (elements M_1 and M_2); tegulum of various forms, with a furrow (Figs 35A–E; 36E) and usually with a delicate apical ledge or lobe (element M_3). *Epigynes*: of various forms; copulatory openings sometimes separated by median guide or septum, often plugged or obscure; introductory ducts variable in length, sometimes lacking; spermathecae often globular, large and dark with fertilisation ducts on posterior margin.

Diagnosis. Male salticids belonging in the subfamily Spartaeinae may be recognised by the presence of a palpal tegular furrow (see p. 140). Females are more difficult and may not always be distinguished in the absence of males, species with small posterior median eyes presenting the most problems, fortunately only two genera *Gelotia* and *Cyrba* are involved. *Gelotia* would not in all probability be recognised in the presence of a mixed group of female salticids, whereas *Cyrba* can even under these circumstances be assigned to Spartaeinae by the unusually long fovea and presence of numerous teeth on the posterior margin of the chelicerae.

Females with large posterior median eyes are slightly less difficult for in practice they can only belong in one of three groups—the Lyssomaninae, Spartaeinae or *Cocalodes*-group. The absence of a lyssomaniform type of carapace and eye pattern (see Wanless, 1980) quickly eliminates lyssomanine genera. But to distinguish between the *Cocalodes*-group and Spartaeinae it is necessary to consult the literature for descriptions and figures of the epigynes. Geographic distribution patterns are of some help as the genera of the *Cocalodes*-group are less widespread—*Cocalodes* and *Allococalodes* Wanless are only known to occur in the Moluccas and New Guinea, *Holcolaetis,* a genus of large flattened spiders is African, whereas *Sonoita,* represented by a single species, is only known from Cape Province, South Africa. A more practicable diagnosis will be presented when all of the *Cocalodes*-group have been revised.

Affinities. The integrity of Spartaeinae is primarily based on the presence of the palpal tegular furrow, but until its degree of development (if any) in other salticids is at least partly understood there is little prospect of determining subfamial relationships which for the presence remain obscure. I am unable to suggest derived characters supporting a sister group relationship with lyssomanine spiders, which as mentioned above may not be monophyletic. Part of the problem stems from the probability that structural elements of the male palpal

organs of lyssomanines have been misinterpreted by myself and other authors, for instance, the element labelled tegulum in Wanless (1980*c*) is almost certainly a modified conductor. The *Cocalodes*-group of genera probably represents another subfamily which seems to be characterised by the form of the median apophysis. The amber salticid discussed below (palp. Figs 1A, B; 2A–C) although closer to the *Cocalodes*-group by virtue of its median apophysis, is similar to Spartaeinae in the form of its tibial apophyses suggesting a possible link between the two groups. Alternatively, some old world lyssomanines possess a pale spot on the tegulum (*Asemonea*) or scale-like protuberance (*Pandisus*) that could represent either a vestigial or germinal median apophysis, thus supporting a *Cocalodes*-group/lyssomanine dichotomy. Broadly speaking, Lyssomaninae, Spartaeinae and the *Cocalodes*-group of genera probably belong to the most plesiomorphic branches of the family; they seem to be related, but the incongruencies cannot be resolved.

The question of intergeneric relations is also difficult as the majority of subfamilies are artificial and polarity assessments based on outgroup comparison with other salticids are largely intuitive. The subject of relationships should perhaps have been put aside until a broader spectrum of salticids has been revised, but in view of recent studies on the optics and behaviour of *Portia,* a brief review of generic affinities is justified, if only to highlight the problems and provide a basis for future criticism.

Spartaeus. The strong ventral spines on legs I and to a lesser extent on legs II appear to be synapomorphic for the genus. But as there are only two known species, only one of which is known from both sexes, I have been unable to detect other derived characters. Its affinities are uncertain.

Yaginumanis. This monotypic genus is difficult to place. It lacks the characters defining other genera and the pleated region of the tegulum M_3 appears to represent its only autapomorphy. The robust retrolateral tibial apophyses of the male palps resemble those of *Portia* and to a lesser extent *Phaeacius.* However I am not sure that we are dealing with a shared synapomorphy as the ancestral state of these heavy apophyses can only be guessed at. The bulbous tegulum, presence of three pairs of ventral spines on metatarsi I, abdominal pattern and reddish black copulatory openings of the epigyne indicate that its affinities could lie near *Spartaeus.*

Taraxella. The broad encircling carapace band and massive tegular apophyses ('x' and 'y') are autapomorphic for this monotypic genus. Its affinities are uncertain, but if apophysis 'x' is homologous with the regular element M_3 then its nearest relative could be *Mintonia.*

Mintonia—Gelotia—Cocalus. These genera present difficulties which I am unable to resolve. Each is supported by synapomorphic male characters viz. *Mintonia* by the form of the tegular ledge M_3 (e.g. Figs 8H; 9C); *Gelotia* by the cap-like retrolateral tibial apophyses (Fig. 20I) and *Cocalus* by the finger-like protuberance resting in the dish-like retrolateral tibial apophysis (Fig. 22C).

Mintonia and *Gelotia* seem to be close as both genera include males whose retrolateral tibial apophyses bear openings. Similar openings are unlikely to occur in *Cocalus,* but unfortunately this does not necessarily support a *Mintonia/Gelotia* sister group as the development of this character is uncertain, it is certainly lacking in *M. ramipalpis* and may not be present in all species of *Gelotia.* On the other hand the general conformation of the palps of *Gelotia* and *Cocalus* is similar, the apical inward curving embolus arising from a lobe-like part of the tegulum in both genera. Furthermore, if the finger-like process of *Cocalus* is analogous with the amorphous process of *Gelotia* (Fig. 20C) then there are possibly stronger reasons for suggesting that *Gelotia* and *Cocalus* are closer than either is to *Mintonia.*

Meleon—Veissella. The hyaline socket of the palpal tibial apophyses is synapomorphic for *Meleon,* while the thin flange-like palpal tibial apophyses and opposing apophyses of the patellae and femora (Fig. 27B, D) are autapomorphic for *Veissella.* They cannot be grouped on the basis of reliable synapomorphies, but their geographical distribution and the general

conformation of the male palps, especially the development of the transverse tegular ledge M_3 (Figs 26G, E; 27G) suggests, that, in spite of their markedly different tibial apophyses, they are closer to one another than to other genera in the subfamily. Their habitus is also similar but probably symplesiomorphic as high carapaces and leg fringes are also characteristic of *Portia* and *Brettus.*

Brettus—Neobrettus—Cyrba. The tubular process lying near or alongside the male palpal retrolatral tibial apophysis (Fig. 33C–E) is synapomorphic for *Brettus* and the slightly bowed legs autapomorphic for *Neobrettus. Cyrba,* however, is not supported by characters which can at present be described as synapomorphic (see remarks p. 185).

The conformation of the male palps, particularly the long slender embolus and open tegular furrow, indicates that the spiders of this heterogenous group are closely allied. Relationships within the group are however uncertain as the alternatives seem to be balanced by an equal number of supposed synapomorphies. The petal-like element of the distal haematodocha M_1 and presence of an embolic guide, a groove on the outside wall of the tegular furrow, supports a *Cyrba/Neobrettus* relationship. On the other hand, *Neobrettus* shares with *Brettus* a subtrapezoid tegulum and basal cymbial modifications which appear to protect the embolic tip. Furthermore, in *Neobrettus* there is a curious minute delicate apophysis (Fig. 24D) which could be a degenerate auxilliary process similar to that of *Brettus.* If this is correct then the case for a *Brettus/Neobrettus* dichotomy is marginally stronger than that between *Cyrba* and *Neobrettus.*

The subapical prolateral origin of the embolus and to a lesser degree the distally sinuous element of the seminal ducts suggests that these genera share affinities with *Portia* and *Phaeacius* and that together they may form a natural group within the subfamily.

Phaeacius—Portia. Whereas *Phaeacius* possesses several uniquely derived characters (pronounced pars pendula, massive retrolateral tibial apophyses and a long filamentous process M_1), *Portia* is, in spite of its distinctive appearance, more difficult to characterise on the same basis. The lateral projecting embolus (Fig. 29A, D) and the large dorsal angular flange on the cymbium being the only synapomorphies which I can suggest at the present time. The well developed tufts and fan-like fringes characteristic of all *Portia* species are probably symplesiomorphic for as mentioned above elements of this ornamentation appear to a lesser extent in other genera.

Their affinities are uncertain for, apart from general similarities in the conformation of the palpal organs, the only derived character which seems to link *Phaeacius* and *Portia* is the large size of the palps. A feature which alone offers only minimal support for the supposed relationship.

Fossil genera

Some of the amber salticids described by Petrunkevitch (1924) are preserved in a mixture of clarite and mineral oil on microscope slides in the collections of the British Museum (Natural History). They are neat and well documented, but an examination of this material has shown that important genitalic characters are largely obscured and not a single species could be reliably placed in the Spartaeinae as defined here. However, the condition of one slide labelled *Eolinus succineus* Petrunkevitch, no. 3782, offered a partial solution to the problem as a fracture line through the amber block indicated that it might be possible to expose the palps which were totally obscured by a crushed carapace. The specimen, originally described as badly damaged (Petrunkevitch, 1942; 424) was easily removed from its clarite mount and cleaned in xylene; pressure from a fine scalpel being sufficient to fracture the block which broke into several pieces revealing a dark, but nevertheless well preserved palp (Fig. 1A–B). This clearly shows that the specimen is not conspecific with *E. succineus* (Fig. 2D) and neither does it entirely agree with published figures of *E. theryi* Petrunkevitch, or *E. tystschenkoi* Prószyński & Zabka. It may represent a new taxon, but of more importance is the fact that the palp appears to possess a median apophysis which looks similar

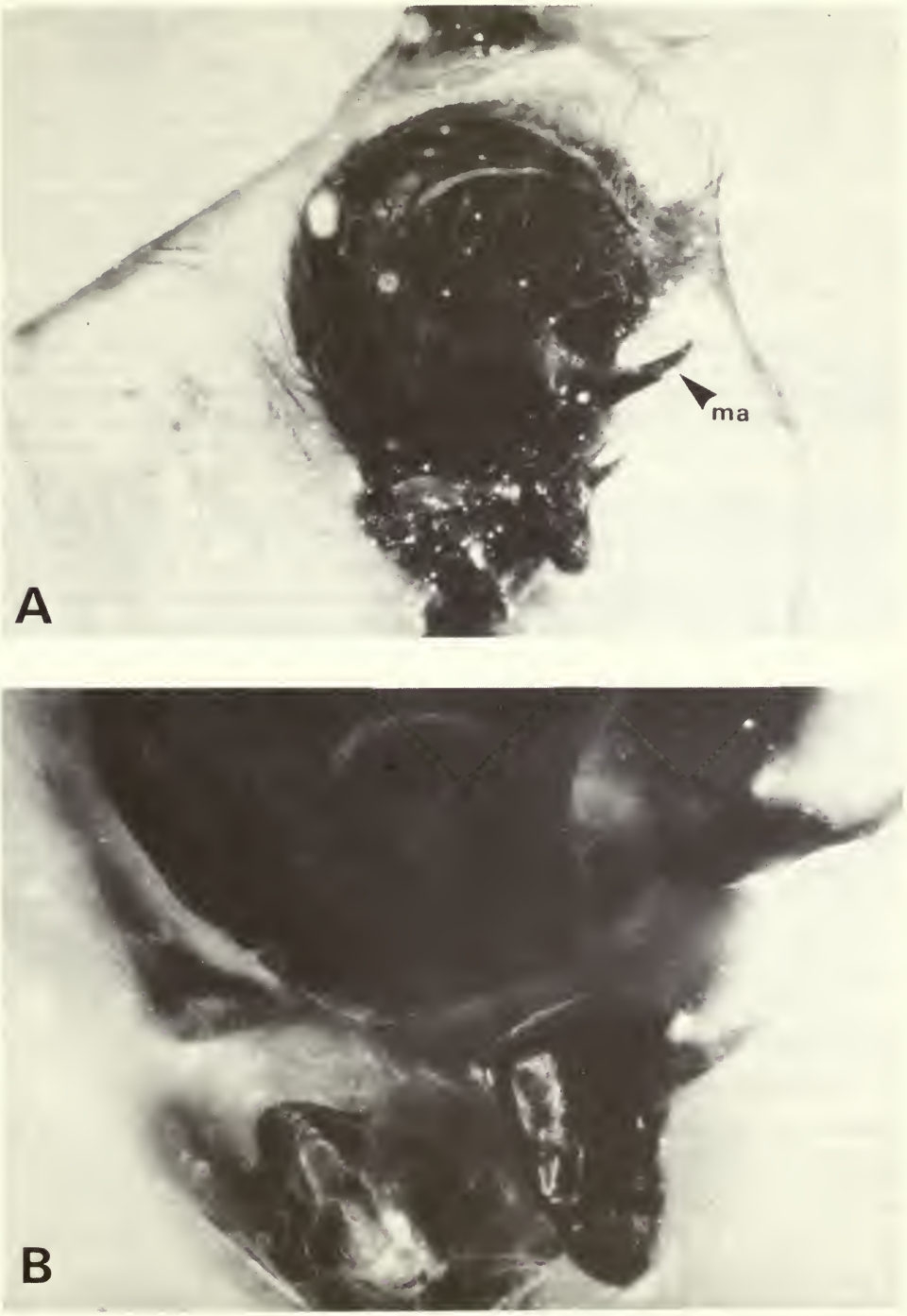

Fig. 1 (A–B) Palp in amber labelled *Eolinus succineus* Petrunkevitch, no. 3782: A, ventral view, note lighter region at base of median apophysis; B, tibia showing ventral and retrolateral apophyses. Abbreviation: ma, median apophysis.

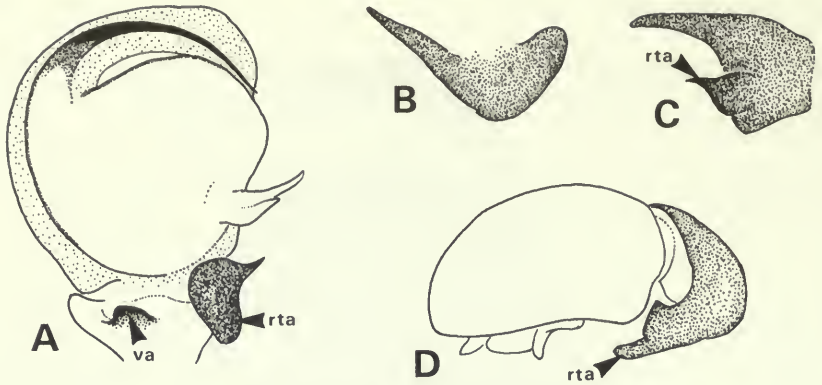

Fig. 2 (A–C) Palp in amber labelled *Eolinus succineus* Petrunkevitch, no. 3782: A, ventral view; B, tibia, dorsal; C, tibiae, retrolateral. D, palp in amber also labelled *Eolinus succineus* Petrunkevitch—slide no. 29126-A, androtype. Note distinct forms of retrolateral tibial apophyses. Abbreviations: rta, retrolateral tibial apophysis, va, ventral apophysis.

to and may be homologous with the median apophysis found in *Cocalodes* (see Wanless, 1982). The paler region around the base of the apophysis (Fig. 1A) could be an artifact of preservation in amber, but it is believed to represent the remains of the basal pleating, chacteristic of some median apophyses. There is no evidence of a tegular furrow which could admittedly be overlooked as the palp is dark. Other interesting features are the dorsal and retrolateral apophyses (Figs 1B; 2A–C), the latter resembling that of *Gelotia* in general form. In addition there is a small ventral apophysis (Fig. 1B) not unlike that found in species of Spartaeinae. In spite of these similarities the absence of a tegular furrow excludes this taxon from this subfamily, its affinities together with those of *E. theryi* and *E. tystschenkoi* probably lie closer to the *Cocalodes*-group.

The relationships of other fossil genera (see Table 2) placed in this subfamily (Petrunkevitch, 1958) have been discussed by Prószyński (1980) and for the present no formal changes are proposed. However, as most recent genera believed to show affinities with amber salticids will have been revised in the fairly near future, a decision should be made as to whether we can justify removing the palps of type specimens from their amber blocks. Modern techniques, considerably less crude than that described above, will minimise the risk of damage but it is clear that unless male palps are examined properly amber specimens will be of limited taxonomic value.

Key to genera of the subfamily Spartaeinae

Females of ***Taraxella*** are unknown.

1 Habitus as in Fig. 24A; highest point of carapace clearly near centre of thoracic part (Fig. 24B) (Bhutan; West Malaysia). . . . . ***NEOBRETTUS*** gen. n. (p. 181)
– Habitus otherwise; highest point of carapace at about level of posterior median eyes . . . 2
2 Male palps with massive apophyses 'x' and 'y' (Fig. 7G) (Sarawak) . . . . ***TARAXELLA*** gen. n. (p. 155)
– Male palps lacking apophyses 'x' and 'y' 3
3 Carapace with low elevation in eye region (Fig. 22A, B); male RTA with sinuous finger-like protuberance (Fig. 22C) (Australia; Indonesia) . . . . . ***COCALUS*** Koch (p. 180)
– Carapace lacking low elevation in eye region; palpal RTA otherwise 4
4 Male palpal patellae and femora with opposing retrolateral apophyses (Fig. 27B, D); epigyne with median guide as in Fig. 27E; (South Africa) . . . . . ***VEISSELLA*** gen. n. (p. 189)
– Male palpal patellae and femora lacking retrolateral apophyses (see note 1); epigynal guide otherwise or lacking 5

5 Male palpal tibiae with flask-like vacuole giving rise to tubular process adjacent to or separate from RTA (Fig. 23D, F); Epigynes with long median introductory ducts; carapace with broad marginal bands of silky white hairs (see note 2) (Burma; India; Madagascar; Sulawesi; Sri Lanka) . . . . . ***BRETTUS*** Thorell (p. 181)

– Male palpal tibiae lacking flask-like vacuole and tubular process; epigyne otherwise; carapace bands if present more irregular (c.f. *Portia*) and comprised of coarser setae 6

6 Male palp with massive RTA (Fig. 28C); distal haematodocha with long filamentous process (Fig. 28A); underside of female coxae IV clothed in minute spatulate setae (Nepal; India; Burma; Singapore; Sumatra; Java; Philippines) . . . . . ***PHAEACIUS*** Simon (p. 190)

– Male palp and coxae otherwise 7

7 Male palpal RTA cap-like in ventral aspect (Figs 17D: 18D; 19F; 20I), sometimes possessing a backward pointing syringe-like apophysis (Fig. 21I); epigynes with thin median ridge (Figs 16F; 17C), or if lacking then apparently with two pairs of rounded spermathecae (Fig. 21C) (see note 3) (Indonesia; Malaysia) . . . . . ***GELOTIA*** Thorell (p. 169)

– Male palpal RTA and female epigyne otherwise 8

8 Posterior median eyes small (PM : PL about 1 : 4) (Ethiopian, Mediterranean and Oriental Regions) . . . . . ***CYRBA*** Simon (p. 185)

– Posterior median eyes relatively large (PM : PL about 3 : 4). 9

9 Legs I with stiff fan-like fringes or if lacking (one Madagascan species) then palpal cymbium with deep basal excavation (see note 4) 10

– Legs I without fan-like fringes 11

10 Very hirsute, abdomen with tufts; anterior eye row weakly to strongly procurved in frontal view; palpal cymbium with pronounced dorsobasal flange (Fig. 29C, E) (Australasian, Oriental and Ethiopian Regions) . . . . . ***PORTIA*** Karsch (p. 191)

– Moderately hirsute, abdomen clothed in minute, often iridescent setae; anterior eye row weakly to strongly recurved in frontal view; palpal tibiae with apophyses arising from membraneous socket (Fig. 26F) (Africa; Madagascar) . . . . . ***MELEON*** gen. n. (p. 186)

11 Tibiae of legs I with numerous long ventral spines (Fig. 5C); chelicerae with 5 or 6 *promarginal* teeth . . . . . ***SPARTAEUS*** Thorell (p. 147)

– Tibiae of legs I with ventral, lateral and usually dorsal spines (see note 5); chelicerae with 3 teeth on prolateral margin 12

12 Male palp with stout RTA, bulbous tegulum and pleated tegular ledge (M_3) (Fig. 6E, J); female epigyne with median blackish red copulatory openings (Fig. 6I) (Japan) . . . . ***YAGINUMANIS*** gen. n (p. 152)

– Male palps with RTA's slender (Figs 8F, 11B, 13B), ramose (Fig. 14B) or bifid (Figs 9C; 12D); tegular element (M^3) a delicate transparent ledge (Fig. 8H) or lobe (Fig. 9C), rarely sclerotised (Fig. 14B); epigynes with rounded spermathecae (Figs 8D; 10F; 12B; 15A) and more or less central copulatory openings (Indonesia; Malaysia) . . . . . ***MINTONIA*** gen. n. (p. 157)

Notes on the keys

1. The male palpal femora of *Gelotia argenteolimbata* (Simon) possesses a large ventral apophysis (Fig. 18C), which may initially be confused with that of *Veissella durbanii* (Peckham & Peckham).

2. It is not certain if silky white carapace bands are present in *Brettus celebensis* (Merian) and *B. madagascarensis* (Peckham & Peckham) which are known only from type specimens. However they are characteristic of Indian and Sri Lankan species and their presence may help to place females in the correct genus.

3. The epigyne of *Mintonia syringopalpis* sp. n., appears at first sight to possess two pairs of spermathecae, but in reality the anterior pair are looped parts of of the introductory ducts.

4. *Meleon madagascarensis* (Wanless) is the only species of the genus without leg fringes. The palp is however quite distinctive and unlikely to be confused with any other (see Wanless, 1978).

5. Females of *Yaginumanis sexdentatus* (Yaginuma) have a single median prolateral spine on tibiae I which could easily be overlooked.

Genus ***SPARTAEUS*** Thorell

Boethus Thorell, 1878: 220. Type species *Boethus spinimanus* Thorell, by original designation and monotypy [junior homonym of *Beothus* Foerster, 1868]. Scudder, 1882, 1: 46; 2: 40. Peckham & Peckham, 1885: 268, 295. Simon, 1901: 400, 401, 402. Petrunkevitch, 1928: 181. Neave, 1939, I: 444. Roewer, 1954: 933. Bonnet, 1955: 892. Wanless, 1978: 85.

Spartaeus Thorell, 1891: 137. Type species *Spartaeus gracilis* Thorell, by original designation and monotypy. Simon, 1901: 401, 402 [=*Boethus*]. Waterhouse, 1902: 347. Petrunkevitch, 1928: 246. Neave, 1940, IV: 230.

Nealces Simon, 1900: 30. Type species *Nealces striatipes* Simon, by original designation. Simon, 1901: 400, 403 [=*Boethus*]. Waterhouse, 1902: 236. Petrunkevitch, 1928: 234. Neave, 1940, III: 273.

Boethuola Strand, 1929: 15 [replacement name for *Boethus* Thorell]. Bonnet, 1955: 892.

DEFINITION. Medium to large spiders ranging from about 4·0 to 8·5 mm in length. Sexual dimorphism not marked, patterns (Figs 4A; 5A) fairly well defined, first pair of legs with numerous long ventral spines on tibiae.

Carapace (Figs 3D; 4B; 5B): moderately high, longer than broad, widest at level between coxae II and III: fovea long and sulciform, apex just behind or level with posterior margins of posterior lateral eyes. *Eyes:* with moderately large lenses set on pronounced tubercles; anteriors subcontiguous with apices slightly recurved in frontal view and recurved in dorsal; anterior medians largest; anterior laterals greater than half diameter of anterior medians; posterior medians relatively large, positioned closer to and inside optical axis of anterior laterals; posterior laterals as large as anterior laterals and set well inside lateral margins of carapace when viewed from above; posterior ocular quadrangle broader than long and wider behind; entire quadrangle occupying about 52 per cent of carapace length. *Clypeus*: moderately low. *Chelicerae*: moderately robust with lateral condyles sometimes strong; inclined anteriorly; parallel or slightly diverging; fang moderately long and curved; promargin with five or six teeth, retromargin with seven to eleven denticles. *Maxillae*: moderately long, slightly diverging with rounded outer distal margins. *Labium:* about as long as broad, half or slightly less than half maxillae length. *Sternum* (Fig. 4D): elongate scutiform. *Abdomen*: elongate ovoid; spinnerets moderately long; posteriors slender and longer than robust anteriors, medians slender and slightly shorter than anteriors. *Legs*: long and slender; first pair with numerous long ventral spines on metatarsi and tibiae, other leg spines weaker; males with femoral organs, a minute tubercle on underside of femora I (Figs 3E; 30A–D); claws pectinate; tufts present; scopulae lacking, but legs I with minute setae (c.f. *Portia*) covering venter of tarsi and forming two rows on metatarsi. *Female palps*: moderately robust with apical claw. *Male palps*: moderately complex with poorly developed interlocking protuberances; patellae with rudimentary anterodorsal tubercle; tibiae with dorso-prolateral tubercle, a slight dorso-retrolateral flange, ventral and retrolateral apophyses, the latter broad with ventral spike; cymbium extended and narrowing distally with apical scopulae and slight retrolateral lobe; embolus moderately long, slender and curved; distal haematodocha forming a membraneous patch M_1 and a translucent prong M_2 containing a sclerotised rod-like structure; tegulum bulbous with peripheral seminal ducts, a short filamentous process M_3 and a crescent-shaped furrow almost completely obscured by the tegulum (Fig. 3A, B); median haematodocha a short broad membraneous tube visible only in expanded palp; subtegulum a pleated and partly sclerotised disc at distal end of basal haematodocha. *Epigyne*: variable, refer to species descriptions.

DIAGNOSIS. From other genera in the subfamily by details of the secondary genitalia and presence of numerous ventral spines on the tibiae of legs I (Figs 3E; 5C). The two known species are easily separated from one another and a key is hardly necessary.

Spartaeus spinimanus (Thorell)
(Figs 3A–F; 4A–G; 30A–D; 33F; 35A)

Boethus spinimanus Thorell, 1878: 221, 309, juvenile. Holotype juvenile Amboina, (MCSN, Genova) [examined]. Thorell, 1881: 431, 705. Simon, 1901: 401, 402. Petrunkevitch, 1928: 181. Roewer, 1954: 933. Bonnet, 1955: 893.

Spartaeus gracilis Thorell, 1891: 6, 137, ♂. Holotype ♂, Sumatra, (UZM, København) [examined]. Roewer, 1954: 933.

Sparthaeus gracilis: Bonnet, 1955: 893 [lapsus calami].

Boethus gracilis (Thorell): Simon, 1901: 402. Reimoser, 1925: 90. Roewer, 1954: 933. Bonnet, 1955: 893. Prószyński, 1971: 385. **Syn. n.**

Nealces striatipes Simon, 1900: 30, ♂. LECTOTYPE ♂ (here designated) Java, (MNHN, Paris) [examined]. Roewer, 1954: 933. Bonnet, 1955: 893.
Boethus striatipes (Simon): Simon, 1901: 401, 402. Roewer, 1954: 933. Bonnet, 1955: 893. Prószyński, 1971: 385. **Syn. n.**
Nealces caligatus Simon, 1900: 30, ♀. LECTOTYPE ♀ (here designated) Sri Lanka, (MNHN, Paris) [examined]. Roewer, 1954: 933. Bonnet, 1955: 893.
Boethus caligatus (Simon): Simon, 1901: 401, 402. Roewer, 1954: 933. Bonnet, 1955: 893. Prószyński, 1971: 385. **Syn. n.**

REMARKS. The general habitus and distinctive spination of legs I suggests that the juvenile type specimen of *Boethus spinimanus* is conspecific with and a senior synonym of *Spartaeus gracilis*. However, in the case of juveniles there is always an element of uncertainty which cannot be overcome until the species and its geographical distribution are well known. Of the other taxa listed in the above synonymy there is no doubt that they are conspecific as the habitus and distinctive secondary genitalic organs are alike.

DIAGNOSIS. *S. spinimanus* is easily distinguished from *S. thailandica* sp. n. by the presence of median epigynal guides in females (Fig. 4E). Males of *thailandica* are unknown.

Male from Sarawak, in fair condition. *Carapace* (Fig. 3D): light brown with blackish mottling on sides and a central tapering yellow-brown band on thoracic part; clothed in recumbent

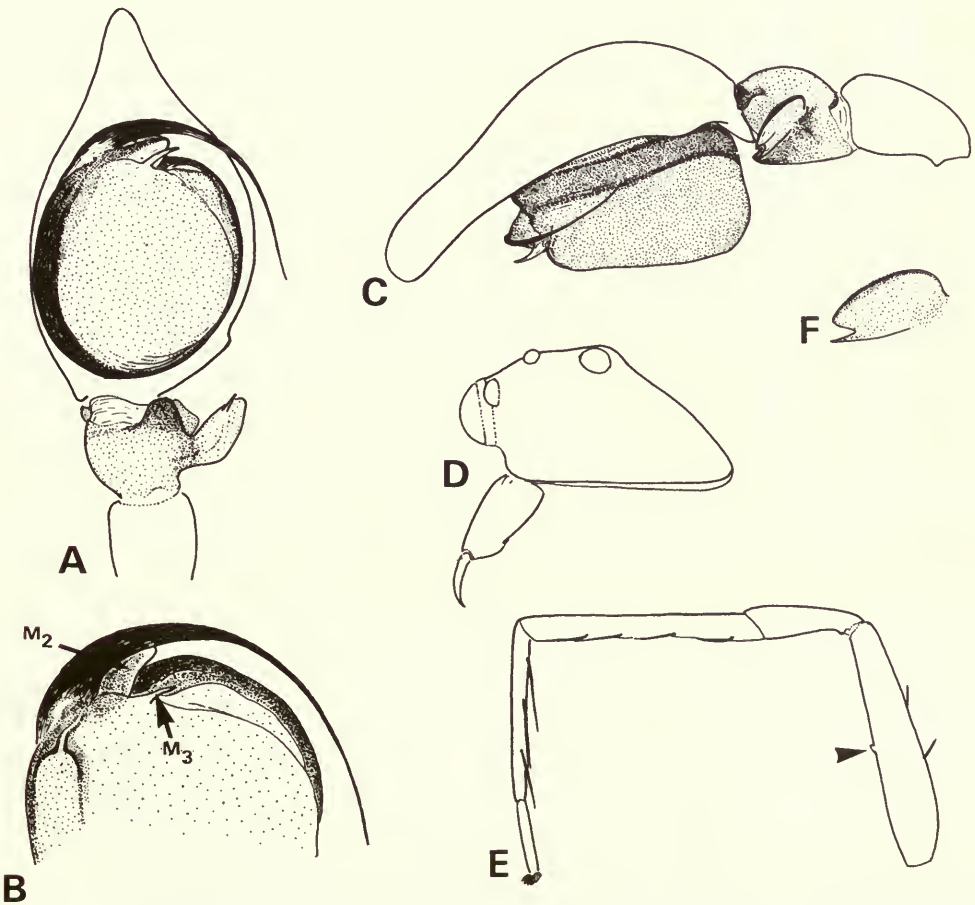

Fig. 3 *Spartaeus spinimanus* (Thorell), ♂: A, palp, ventral; B, distal half of tegulum; C, palp, retrolateral; D, carapace, lateral; E, leg I; F, retrolateral tibial apophysis.

brown and whitish hairs, shiny under some angles of illumination. *Eyes*: with black surrounds; fringed by whitish hairs. *Clypeus*: thinly clothed in light brown and whitish hairs. *Chelicerae*: yellow-brown with sooty markings and scattered fine brown hairs; promargin with five teeth, retromargin with seven denticles. *Maxillae and labium*: pale yellow-brown. *Sternum*: pale yellow-brown with darker margins; shiny with scanty clusters of short stiff light brown hairs opposite coxae. *Coxae*: pale yellow-brown, shiny. *Abdomen*: yellow-brown with blackish lateral mottling; dorsum and sides covered in fine recumbent pale brown/iridescent lanceolate hairs with testaceous ones on venter; anal tubercle and spinnerets pale yellow, the latter with sooty lateral stripes on anterior and posterior pairs. *Legs*: long and slender with numerous spines (strongest on legs I) and femoral organ, a small tubercle on underside of femoral I (Figs 3E; 30A–D); legs I with tarsi pale yellow, metatarsi, tibiae and patellae yellow-brown tinged black on lateral sides, femora pale yellow with black lateral stripes; other legs similar, but with longitudinal bands of short pale amber hairs particularly on femora, and vague sooty annuli on metatarsi III and IV. Spination of legs I: metatarsi v 2-2-2; tibiae 3-4-3; femora p 0-1-0, d 1-1-2, r 0-1-0. *Palp* (Figs 3A–C; 33F; 35A).

Dimensions (mm): total length 4·7; carapace length 2·08, breadth 1·72, height 1·28; abdomen length 2·56; eyes, anterior row 1·54, middle row 1·12, posterior row 1·39; quadrangle

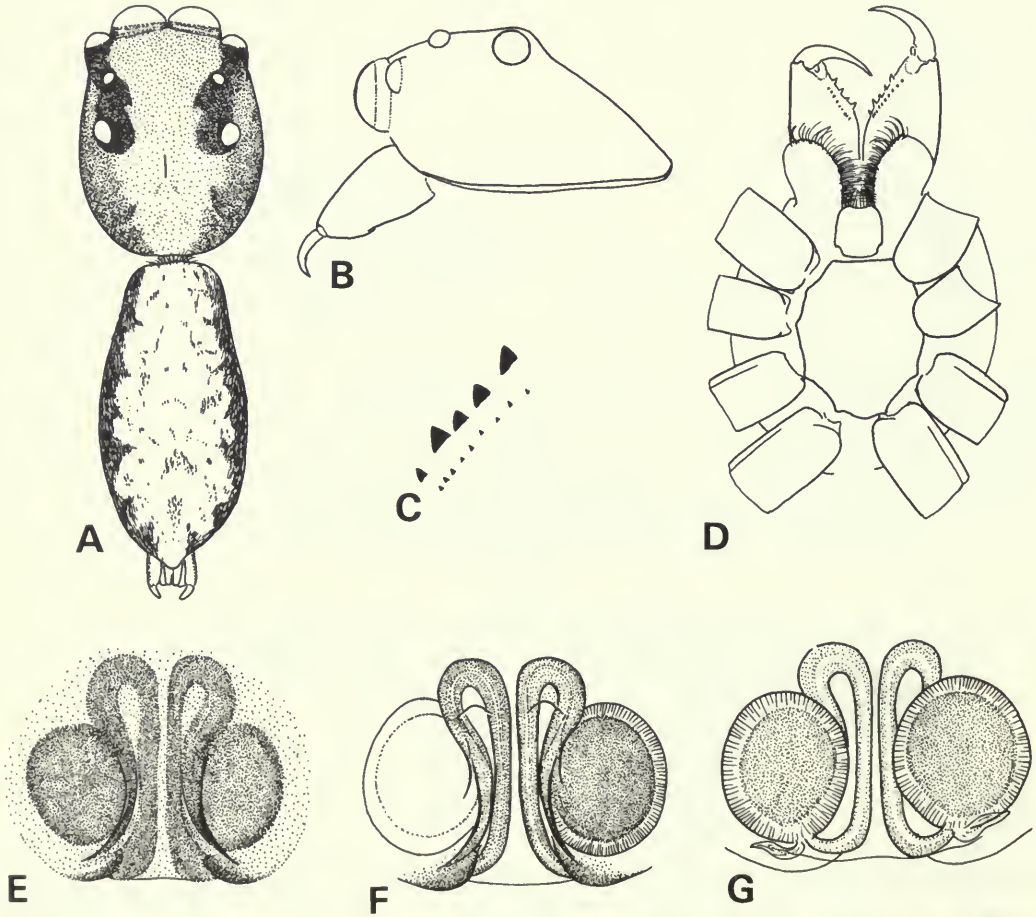

Fig. 4 *Spartaeus spinimanus* (Thorell), ♀: A, dorsal; B, carapace, lateral; C, cheliceral teeth, inner view; D, mouthparts, sternum and coxae; E, epigyne; F, vulva, outer view; G, vulva, inner view.

length 1·2 (57 per cent of carapace length). *Ratios:* AM : AL : PM : PL :: 12·5: 7·5 : 4·5 : 7; AL–PM–PL :: 6·5 : 8; AM : CL :: 12·5 : 3.

Female from Java (in same vial as lectotype ♂ of *Nealces striatipes*), in fair condition. Similar to ♂ except for the following: colour markings more clearly defined, possibly an artifact of preservation. *Chelicerae* (Fig. 4C): more robust than in ♂; orange-brown with sooty markings; sparsely clothed in brownish hairs; promargin with five teeth, retromargin with nine denticles. *Abdomen* (Fig. 4A): pale yellow clothed in creamy white hairs with vague sooty markings above and blackish mottling covered in dark amber hairs on sides; below, an indistinct band of short pale amber hairs from epigyne to spinnerets. *Legs*: legs and especially spines of legs I more robust than in ♂; legs I pale yellow with sooty metatarsi, other legs similar, but metatarsi with vague annuli. *Palps*: yellow-brown with tarsi orange-brown tinged black distally; clothed in pale yellowish, and light amber hairs. *Epigyne* (Figs 4E–G): dark reddish brown, relatively large.

Dimensions (mm): total length 5·44; carapace length 2·42, breadth 2·04; height 1·4; abdomen length 3·12; eyes, anterior row 1·8, middle row 1·38, posterior row 1·68; quadrangle length 1·28 (52 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 15 : 9 : 5 : 8·5; AL–PM–PL :: 7–10; AM : CL :: 15 : 3.

VARIATION. ♂ total length varies from 4·2 to 5·8 mm, carapace length 2·0–2·5 mm (five specimens). ♀ total length 5·4–6·3 mm, carapace length 2·38–2·5 mm (five specimens). One male, the type of *N. striatipes,* has a dark orange carapace with the thoracic band poorly defined, also the distal extension of the cymbium is slightly more elongate and narrow. In some males the seminal duct is more clearly defined in the region of the embolic base.

DISTRIBUTION. Indonesia: Amboina, Java and Sumatra; Malaysia: Sarawak; Singapore; Sri Lanka.

MATERIAL EXAMINED. **Amboina:** holotype [of *Boethus spinimanus*], a juvenile, (MCSN, Genova). **Java**: Palabuan, lectotype ♂ [of *Nealces striatipes*], 2♀♀ not types, *Fruhstorfer* (MNHN, Paris, 20328). **Sumatra**: Padang, holotype ♂, [of *Spartaeus gracilis*], *P. A. Klein,* (UZM, København); Padang, 1♀, ix.1913, *E. Jacobson,* (RNH, Leiden. 540). **Sarawak**: Marudi, on outside wall of house, 1♂, 26.iv.1978, *F. R. Wanless,* R.G.S./Sarawak Government Mulu Expedition, (BMNH). **Singapore**: 1♂, *H. N. Ridley*, (BMNH). **Malaya**: 1♂, 1♀, no other data, (BMNH). **Sri Lanka**: Galle, lectotype ♀, [of *Nealces caligatus*], with one juvenile specimen, *E. Simon,* (MNHN, Paris, 20537).

Spartaeus thailandica sp. n.
(Fig. 5A–D)

DIAGNOSIS. Distinguished from *S. spinimanus* by the absence of pronounced median epigynal guides (Fig. 5D).

Male. Unknown.

Female holotype, in poor condition. *Carapace* (Fig. 5A, B): dark mahogany with light yellow-brown thoracic markings and more or less contiguous lateral blotches; thinly clothed in recumbent fine whitish hairs. *Eyes*: with blackish surrounds except anterior medians; fringed by whitish hairs. *Clypeus*: with scattered light brown hairs. *Chelicerae*: dark mahogany, shiny with scattered dark brown hairs; promargin with six teeth, retromargin with 11. *Maxillae*: amber with inner distal margins yellow-brown. *Labium*: brown-black grading to amber distally. *Sternum*: yellow-brown with dark amber margins; clothed in pale yellow-brown hairs. *Coxae*: yellow-brown. *Abdomen*: dirty pale yellow-brown with blackish markings, ventrally a broad sooty band from epigyne to spinnerets; mostly rubbed, but areas clothed in fine whitish hairs with scattered flecks of pale amber ones. *Legs*: long and slender; legs I (Fig. 5C), pale yellow-brown with metatarsi and tibiae dark amber and ventrally strongly spinose; legs II similar but metatarsi and tibiae paler with fewer and weaker ventral spines; other

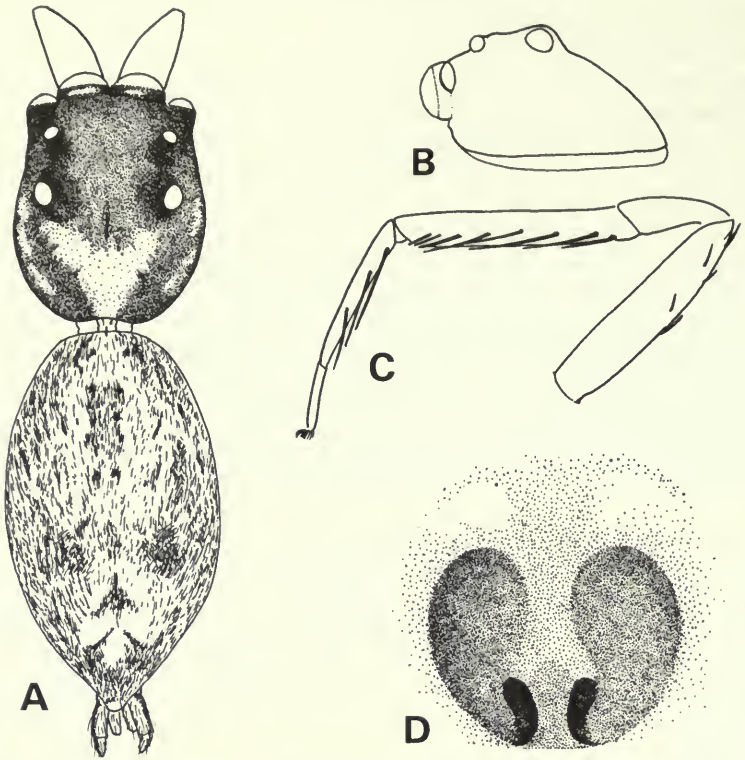

Fig. 5 *Spartaeus thailandica* sp. n., holotype ♀: A, dorsal; B, carapace, lateral; C, leg I; D, epigyne.

legs pale yellow-brown with vague sooty annuli. Spination of legs I: metatarsi v 2-2-1, p 0-0-1; tibiae v 6-4-6; femora p 0-1-1, d 0-2-1. *Palps*: pale yellow with dark amber tarsi and tibiae. *Epigyne* (Fig. 5D): thinly clothed in fine hairs, vulva not examined.

Dimensions (mm): total length 8·4; carapace length 3·2, breadth 2·72, height 2·08; abdomen length 5·08; eyes, anterior row 2·44, middle row 1·96, posterior row 2·18; quadrangle length 1·64 (51 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 18 : 11 : 8 : 11; AL–PM–PL :: 8–15; AM : CL :: 18 : 5.

DISTRIBUTION. Thailand.

MATERIAL EXAMINED. **Thailand**: Dui Sutep, 1100 m, holotype ♀, 13.i.1959 (*B. Degerbøl*) (UZM. København, Pr. 2110).

Genus *YAGINUMANIS* gen. n.

DEFINITION. Medium to large spiders ranging from about 7·0 to 9·6 mm in length. Sexual dimorphism not marked, patterns fairly well defined (Fig. 6A).

Carapace (Fig. 6A, C): moderately high, longer than broad, widest at level between coxae II and III; fovea long and sulciform, apex almost level with posterior margin of posterior lateral eyes. *Eyes*: with moderately large lenses set on moderately pronounced tubercles; anteriors subcontiguous with apices more or less level in frontal view and moderately recurved in dorsal; anterior medians largest; anterior laterals more than half diameter of anterior medians; posterior medians relatively large, positioned closer to and more or less on optical axis of anterior laterals; posterior laterals as large as anterior laterals and positioned inside lateral margins of carapace when viewed from above; posterior ocular quadrangle broader than long and wider behind; entire quadrangle about 45 per cent of carapace

length. *Clypeus*: of medium height. *Chelicerae*: moderately robust with strong lateral condyles; more or less parallel and slightly inclined anteriorly; fang moderately robust and curved; promargin with three teeth, retromargin with five or six denticles. *Maxillae*: moderately long, slightly diverging with outer distal margins rounded. *Labium*: about as long as broad and about half maxillae length. *Sternum* (Fig. 6D): elongate scutiform. *Abdomen*: elongate ovoid with four indistinct apodemal spots; spinnerets moderately long, posteriors moderately robust and slightly longer than robust anteriors, medians slender and shorter than anteriors. *Legs*: moderately long and slender, in females first pair slightly more robust; spines numerous and moderately strong; claws pectinate, tufts present; scopulae absent. *Male palps*: fairly large, dark and moderately complex with poorly developed interlocking protuberances; patellae with rudimentary anterodorsal tubercle; tibiae with robust ventral and retrolateral apophyses, the latter bearing a strong lobe; cymbium with distal scopulae, a small basal tubercle and slight lobe on retrolateral margin; embolus short, slender and arising distally; distal haematodocha a membraneous patch (M_1); tegulum bulbous with peripheral seminal ducts a pleated distal element M_3 and an irregular sclerotised pit-like furrow; median haematodocha, subtegulum and basal haematodocha not examined. *Epigyne*: moderately distinct and protruding with some frilling anteriorly; median openings obscured by blackish red surrounds; introductory ducts short, wide and poorly defined; spermathecae also ill-defined, somewhat pear-shaped with posterior portion partly rolled-up and bearing fertilisation ducts.

TYPE SPECIES. *Boethus sexdentatus* Yaginuma.

ETYMOLOGY. Named in honour of Dr Takeo Yaginuma; the gender is masculine.

DIAGNOSIS. From other genera in the subfamily by details of the secondary genitalia (Fig. 6E, G–I, J) and geographical distribution.

Yaginumanis sexdentatus (Yaginuma) comb. n.
(Fig. 6A–J)

Boethus sexdentatus Yaginuma, 1967: 54, holotype ♀, paratype ♂, Ohtemon-Gakuin University, Osaka [not examined]. Shinkai & Hara, 1975: 16. Matsumoto, Shinkai & Ono, 1976: 95; Yaginuma, 1977: 398.

DIAGNOSIS. By geographical distribution, the structure of the palp in males (Fig. 6E, J) and by the presence of dark reddish copulatory openings on the posterior margin of the protruding epigynal plate in females (Fig. 6I).

REMARKS. Yaginuma's original description is excellent and the species is redescribed here only for the sake of completeness.

Male from Idzu, in fair condition. *Carapace*: cephalic part and thoracic sides dark amber lightly tinged and mottled black with middle of thorax paler, more or less as in (Fig. 6A); clothed in fine whitish hairs with brownish ones on sides. *Eyes*: with black surrounds except anterior medians; fringed by whitish hairs. *Clypeus*: clothed in fairly coarse pale amber hairs and edged with scattered long brownish ones. *Chelicerae*: orange-brown with sooty markings on basal and middle regions; thinly clothed in long fine whitish, and pale brown hairs; promargin with three teeth, retromargin with five or six denticles. *Maxillae and labium*: yellow-brown with inner distal margins of maxillae and labial tip whitish. *Sternum*: pale yellow-brown with slightly darker margins; thinly clothed in fine pale hairs. *Coxae*: pale yellow-brown. *Abdomen*: generally pale yellow-brown with vague sooty markings; dorsum clothed in recumbent fine whitish hairs interspersed with scattered stiff pale amber ones, upper sides clothed in short dark brownish hairs forming a pattern as shown in (Fig. 6A), lower sides clothed in fine whitish hairs with venter dark greyish clothed in fine pale amber ones; spinnerets yellow-brown with some black on outer sides of anteriors and posteriors. *Legs*: generally yellow-brown with indistinct annuli on metatarsi III and IV; spines moderately strong and numerous. Spination of legs I: metatarsi v 2-2-2, p 0-0-1, r 0-0-1; tibiae

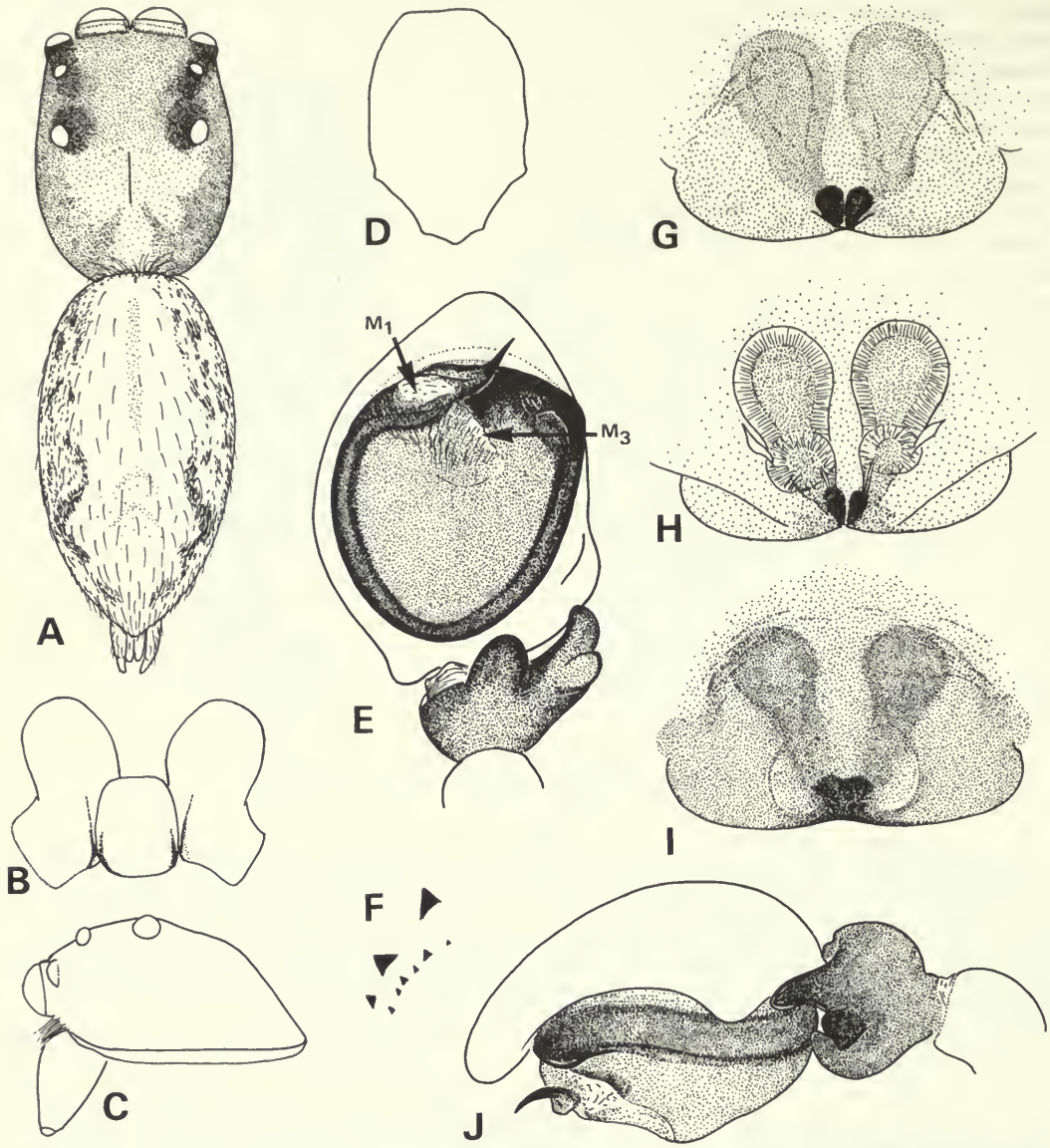

Fig. 6 *Yaginumanis sexdentatus* (Yaginuma), ♂: E, palp, ventral; F, cheliceral teeth, inner view; J, palp, retrolateral; ♀: A, dorsal; B, maxillae and labium; C, carapace, lateral; D, sternum; G, vulva, outer view; H, vulva inner view; I, epigyne.

v 2-2-2, p 0-1-1, d 1-1-0, r 0-1-1; patellae p 0-1-0, r 0-1-0; femora p 0-0-1, d 0-2-4. *Palp* (Fig. 6E, J).

Dimensions (mm): total length 6·96; carapace length 3·12, breadth 2·32, height 1·64; abdomen length 3·8; eyes, anterior row 1·98, middle row 1·74, posterior row 1·84; quadrangle length 1·36 (43 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 15·5 : 9 : 6·5 : 9; AL–PM–PL :: 8–12; AM : CL :: 15·5 : 6.

Female from Idzu, in fair condition. Essentially similar to ♂ except for the following: *Carapace*: with paler indistinct and uneven marginal band from clypeus to level of coxae II–III. *Clypeus*: clothed in long white hairs. *Chelicerae*: amber with median sooty transverse band;

shiny; thinly clothed in fine pale amber hairs; promargin with three teeth retromargin with five. *Legs*: spination of legs I: metatarsi v 2-2-2; tibiae v 2-2-2, p 0-1-0; femora p 0-0-1, d 0-2-3. *Palps*: femora and patellae yellow-brown with whitish hairs, tibiae and tarsi yellow-brown with yellow-brown hairs. *Epigyne* (Figs 6G–I): clothed in fine whitish hairs.

Dimensions (mm): total length 7·12; carapace length 3·08, breadth 2·36, height 1·68; abdomen length 4·12; eyes, anterior row 2·04, middle row 1·76, posterior row 1·91; quadrangle length 1·4 (45 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 15·5 : 9 : 6·5 : 9; AL–PM–PL :: 7–12; AM : CL :: 15·5 : 6.

VARIATION. Another ♂ measures 6·3 mm total length, 2·76 mm carapace length, while ♀♀ vary from 6·96 to 9·6 mm total length, 2·84–3·16 mm carapace length (seven specimens).

DISTRIBUTION. Japan.

MATERIAL EXAMINED. **Japan,** Idzu, Shizuoka Prefecture (nr. Mt. Fuji), 2♂♂, 7♀♀, (purchased from *S. Akiyama,* 5.vi.1910) (BMNH. 1911.12.12.208–366 part).

Genus *TARAXELLA* gen. n.

DEFINITION. Spiders of medium size, i.e. between 4·0 and 8·0 mm in length. Males with conspicuous markings (Fig. 7A), but extent of sexual dimorphism unknown.

Carapace (Fig. 7A, B): high, longer than broad, widest at level of coxae II; fovea long and sulciform, apex level with centre of posterior median eyes; clearly marked with broad encircling band. *Eyes*: with large lenses set on moderately well developed tubercles; anteriors contiguous with apices weakly procurved in frontal view and moderately recurved in dorsal; anterior medians largest; anterior laterals more than half diameter of anterior medians; posterior medians relatively large, positioned slightly closer to and more or less on optical axis of anterior laterals; posterior laterals as large as anterior laterals and positioned inside lateral margins of carapace when viewed from above; posterior ocular quadrangle broader than long and wider behind; entire quadrangle about 57 per cent of carapace length. *Clypeus*: moderately high. *Chelicerae*: moderately robust; inclined anteriorly and slightly divergent; fang moderately slender and curved; promargin with six or seven teeth, retromargin with eight or nine denticles. *Maxillae*: moderately long, more or less parallel with outer distal margins rounded. *Labium*: longer than broad and about half maxillae length. *Sternum* (Fig. 7E): elongate scutiform. *Abdomen*: elongate avoid; spinnerets moderately long, posteriors moderately robust and more or less as long as robust anteriors, medians slender and slightly shorter than anteriors. *Legs*: moderately long and slender; spines numerous and moderately strong; claws pectinate; tufts present; scopulae absent. *Female palps*: unknown. *Male palps*: moderately large and complex with dorsal interlocking tubercle and recess on tibiae/cymbial joint; femora slightly bowed; patellae with slight anterodorsal tubercle; tibiae slightly excavated retrolaterally, with anterodorsal tubercle, a large ventral apophysis and retrolateral apophysis bearing a lightly sclerotised flange, also, between ventral and retrolateral apophyses a tuft of stout setae; cymbium with distal scopulae and basal depression opposite tibial anterodorsal tubercle; embolus short, slender and arising apically, but largely hidden by apophysis 'x' and anterior margin of tegular furrow; distal haematodocha forming a white membraneous area M_1 bearing a large delicate fan-shaped process, another membraneous region (?) M_2 lies between apophyses 'x' and 'y'; tegulum bulbous with peripheral seminal ducts looping distally, massive apophyses 'x' and 'y' the latter possibly homologous with M_3 and a heavily sclerotised crescent-shaped furrow; median haematodocha, subtegulum and basal haematodocha not examined. *Epigynes*: unknown.

TYPE SPECIES. *Taraxella solitaria* sp. n.

ETYMOLOGY. The genus name is an arbitrary combination of letters; the gender is considered to be feminine.

DIAGNOSIS. Distinguished from other genera in this subfamily by the presence of palpal apophyses 'x' and 'y' (Fig. 7G) and encircling carapace band (Fig. 7A).

Taraxella solitaria sp. n.
(Fig. 7A–G)

DIAGNOSIS. By the broad encircling carapace band and massive palpal tegular apophyses 'x' and 'y' (Fig. 7G).

Female. Unknown.

Male holotype, in good condition. *Carapace* (Fig. 7A, B): orange-brown suffused and mottled black with broad encircling creamy white band; irregularly clothed in dark amber hairs, mostly rubbed, with a few fine whitish ones in the encircling band. *Eyes*: with black surrounds except anterior medians; fringed by amber hairs with whitish ones around anteriors. *Clypeus*: pale yellow with broad vertical black bands below anterior median eyes; shiny. *Chelicerae*: amber suffused and mottled black with inner basal region grading to yellow-brown; shiny; thinly clothed in brownish hairs; promargin with six or seven teeth, retromargin with eight or nine. *Maxillae and labium* (Fig. 7D): yellow-brown. *Sternum*: (Fig. 7E): pale yellow with darker margins; thinly clothed in brownish hairs. *Coxae*: pale yellow-brown, anteriors faintly tinged with some black. *Abdomen*: yellow-brown tinged and mottled black; clothed in dark amber hairs particularly on sides; spinnerets whitish yellow with

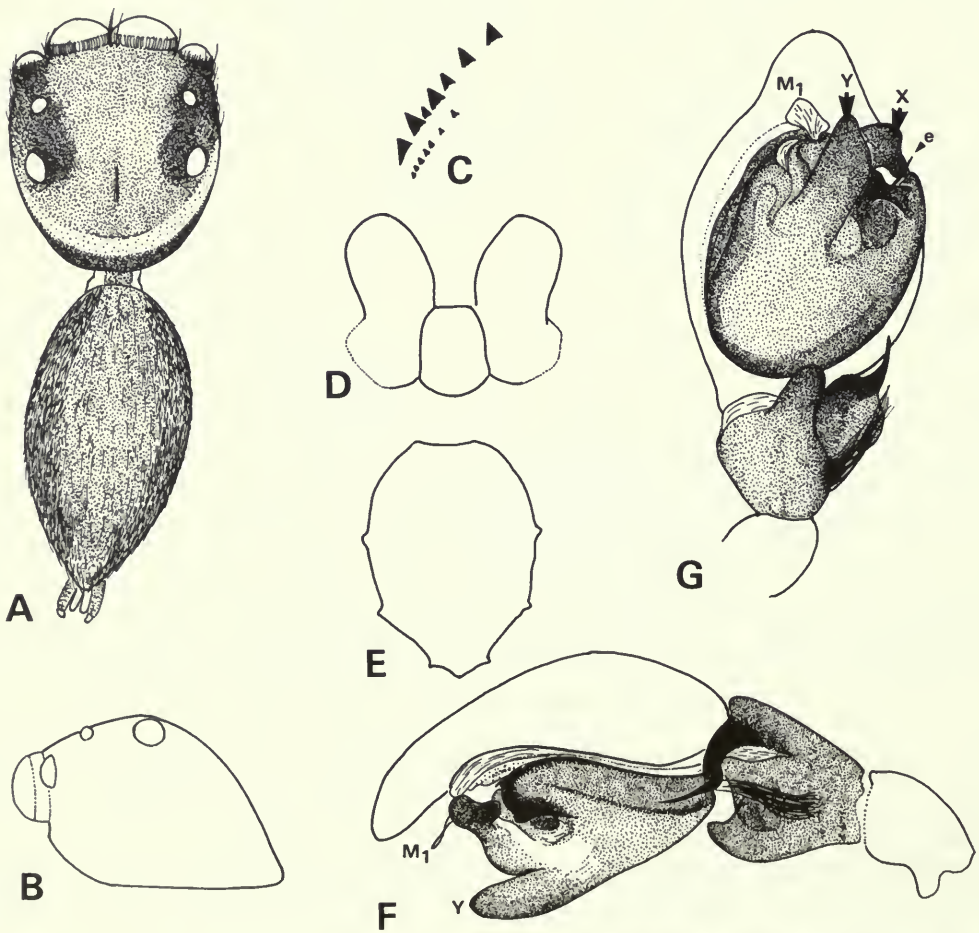

Fig. 7 *Taraxella solitaria* sp. n., holotype ♂: A, dorsal; B, carapace, lateral; C, cheliceral teeth, inner view; D, maxillae and labium; E, sternum; F, palp, retrolateral; G, palp, ventral. Abbreviation: e, embolus.

anteriors and posteriors tinged black. *Legs*: moderately long and slender with numerous spines; generally yellow-brown with blackish femora and vague blackish annuli on metatarsi and tibiae. Spination of legs I: metatarsi v 2-1-1, p 1-2-1, d 0-0-2, r 1-0-0; tibiae v 2-2-2, p 1-0-1, d 2-1-0, r 0-0-1; patellae p 0-1-0; femora d 0-2-4. *Palp* (Fig. 7F, G): the embolus can be seen just protruding beyond the edge of apophysis 'x' (arrowed, Fig. 7G).

Dimensions (mm): total length 6·0; carapace length 2·64; breadth 2·16, height 1·88; abdomen length 3·2; eyes, anterior row 2·18, middle row 1·8, posterior row 2·04; quadrangle length 1·52 (57 per cent of carapace length). *Ratios*: AM : AL : PM : PL ::18 : 10 : 6 : 10; AL–PM–PL :: 9–9·5; AM : CL :: 18 : 6.

DISTRIBUTION. East Malaysia, Sarawak.

MATERIAL EXAMINED. **Sarawak,** Gunung Mulu National Park, Melinau Gorge, under dead wood in limestone forest, holotype ♂, 1.v.1978 (*F. R. Wanless*, R.G.S./Sarawak Government Expedition) (BMNH, 1982.1.11.1).

Genus *MINTONIA* gen. n.

DEFINITION. Spiders small to medium in size, i.e. total length between 2·0 and 8·0 mm. Markings sometimes distinctive, but extent of sexual dimorphism uncertain as most species only known from one sex.

Carapace: moderately high, longer than broad, widest at level between coxae II–III: fovea long and sulciform, apex near centre or posterior margin of posterior lateral eyes. *Eyes*: with moderately large lenses set on low tubercles; anteriors more or less contiguous with apices level or slightly procurved in frontal view and moderately recurved in dorsal; anterior medians largest; anterior laterals greater than half diameter of anterior medians; posterior medians relatively large, positioned closer to and on or near optical axis of anterior laterals; posterior laterals about as large as anterior laterals and set inside lateral margins of carapace when viewed from above; posterior ocular quadrangle broader than long and wider behind; entire quadrangle occupying between 48 and 62 per cent of carapace length. *Clypeus*: low to moderately high. *Chelicerae*: small to medium in size, slightly more robust in female; slightly inclined anteriorly and more or less parallel; fang moderately strong and curved; promargin with three teeth, retromargin with five to seven denticles. *Maxillae*: moderately long, generally parallel with rounded outer distal margins. *Labium*: as long as broad or slightly longer than broad, about half maxillae length. *Sternum* (Figs 8B; 10E): more or less elongate scutiform. *Abdomen*: elongate ovoid; spinnerets moderately long, posteriors slender and sometimes longer than robust anteriors, medians slender and slightly shorter than anteriors. *Legs*: moderately long and slender, first and second pairs slightly more robust in females; males usually with femoral organ, a minute amber spot or tubercle on underside of femora I; spines numerous and moderately strong; claws pectinate; tufts present, scopulae absent. *Female palps*: moderately robust with distal claw. *Male palps*: moderately complex and interspecifically distinct, moderately hirsute with dorsal interlocking tubercles weak or lacking on cymbial/tibial joint and weak to pronounced on patellae; tibiae more or less excavated retrolaterally with moderately large ventral apophyses and complex retrolateral apophyses of various forms, some with secretory openings; cymbium with distal scopulae, sometimes modified distally to accommodate embolic region or basally to protect retrolateral apophysis; embolus of various forms arising apically; distal haematodocha forming poorly defined membraneous region M_1 which is often only apparent in prolateral view, region M_2 either apparently lacking or bearing a slender delicate process (Fig. 8H); tegulum usually subovoid with peripheral seminal ducts, a delicate translucent ledge or lobe-like process M_3 rarely sclerotised, and usually with a small lightly sclerotised crescent-shaped furrow; median haematodocha a membraneous sac only evident in expanded palps, subtegulum a ring-like sclerite at distal end of basal haematodocha (examined only in *M. ramipalpis*). *Epigynes*: interspecifically distinct; sometimes with anterolateral frilling; opening positioned centrally with or without a short median septum and sometimes with sclerotised posterior margin;

introductory ducts not evident; spermathecae rounded with fertilisation ducts on posterior margins.

TYPE SPECIES. *Mintonia tauricornis* sp. n.

ETYMOLOGY. The genus name is an arbitrary combination of letters; the gender is considered to be feminine.

DIAGNOSIS. Males by the development of the palpal tegular ledge M_3, e.g. (Figs 8H: 9C; 12E; 14B). Females with more difficulty by details of the epigynes.

Key to species of *Mintonia*

Males (those of ***nubilis*** unknown)

1 Embolus with pronounced basal prong (Fig. 11C arrowed) (Singapore) . . . ***protuberans*** sp. n. (p. 162)
– Embolus without basal prong 2
2 RTA long and sinuous with short lateral prong (Fig. 14B) (Java, Sarawak, Sumatra) . . . ***ramipalpis*** (Thorell) (p. 166)
– RTA otherwise 3
3 RTA comprised of two long slender prongs (Fig. 9C) (Kalimantan) . . ***mackiei*** sp. n. (p. 160)
– RTA otherwise 4
4 RTA with lateral lobe or condyle (Fig. 13B arrowed) (Sarawak) . ***melinauensis*** sp. n. (p. 165)
– RTA otherwise 5
5 RTA long slender and curving (Fig. 8F) (Sarawak) . . . . . ***tauricornis*** sp. n. (p. 158)
– RTA robust, distally bifid (Fig. 12D) (Sarawak) . . . . . ***breviramis*** sp. n. (p. 164)

Females (those of ***mackiei, melinauensis*** and ***protuberans*** are unknown)

1 Epigyne with thin dark median ridge (Fig. 10F) (Kalimantan). . . . ***nubilis*** sp. n. (p. 161)
– Epigyne without thin dark median ridge. 2
2 Epigynal opening with blackish T-shaped mark or blotch (Fig. 15A) (Java, Sarawak, Sumatra) . . . ***ramipalpis*** (Thorell) (p. 168)
– Epigynal opening without T-shaped mark or blotch 3
3 Posterior rim of epigynal opening resembling buffalo horns (Fig. 8D) (Sarawak) . . . ***tauricornis*** sp. n. (p. 159)
– Posterior rim of epigynal opening tube-like and curving (Fig. 12B) (Sarawak) . . . ***breviramus*** sp. n. (p. 165)

Mintonia tauricornis sp. n.
(Figs 8A–H; 32E, F; 35B)

DIAGNOSIS. Distinguished by the curved retrolateral tibial apophysis in males (Figs 8F, H), and by the horn-like rim of the epigynal opening in females (Fig. 8D).

Male holotype, in fair condition. *Carapace* (Fig. 8G): dark orange-brown lightly tinged black in eye region with vague yellowish brown markings on thoracic part; shiny and weakly iridescent under some angles of illumination; irregularly clothed in recumbent black lanceolate hairs on sides of thorax, otherwise rubbed. *Eyes*: with black surrounds except anterior medians; ventral rim of anterior row fringed by whitish hairs, otherwise rubbed. *Clypeus*: yellow-brown edged black; thinly covered in light brownish hairs below anterior medians with dense fringes of long white hairs below anterior laterals and outer margins of anterior medians which sweep inwards covering cheliceral bases. *Chelicerae*: yellow-brown, shiny; basal half densely white haired; promargin with three teeth retromargin with seven. *Maxillae and labium*: pale yellow-brown lightly tinged with some black. *Sternum*: shape more or less as in ♀; pale yellow with darker margins; thinly clothed in fine hairs. *Coxae*: pale yellow. *Abdomen*: similar to ♀, but more slender; pale yellow; rubbed. *Legs*: moderately long and slender with numerous spines and minute pale amber spot (femoral organ) on under side

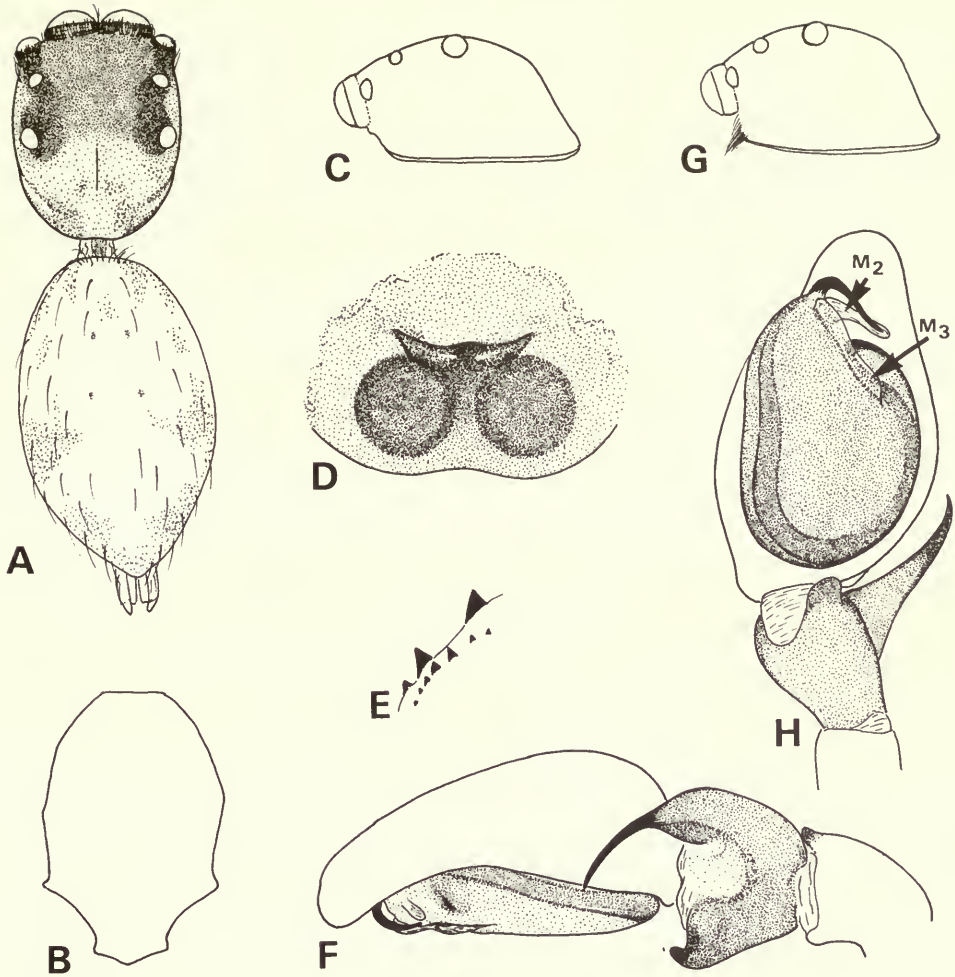

Fig. 8 *Mintonia tauricornis* sp. n., holotype ♂: F, palp, retrolateral; G, carapace, lateral; H, palp, ventral. Paratype ♀: A, dorsal; B, sternum; C, carapace, lateral; D, epigyne; E, cheliceral teeth, inner view.

of femora I; generally yellow-brown becoming darker distally except for femora I which is suffused with black and tibiae III which has a black proventral stripe. Spination of legs I: metatarsi v 2-2-0, p 1-0-1, d 0-1-0, r 1-0-1; tibiae v 2-3-2, p 0-1-0, d 3-3-0; patellae p 0-1-0, r 0-1-0; femora d 0-2-4. *Palp* (Figs 8F, H; 32E, F; 35B): the lobe M_2 is not as conspicuous as illustrated.

Dimensions (mm): total length 4·48; carapace length 2·04, breadth 1·8, height 1·4; abdomen length 2·44; eyes, anterior row 1·68, middle row 1·44, posterior row 1·64; quadrangle length 1·24 (60 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 13·5 : 8 : 4·8 : 7·5; AL–PM–PL :: 7·5–10; AM : CL :: 13·5 : 5.

Female paratype, in fair condition. *Carapace* (Fig. 8A, C): eye region amber tinged black, sides and thorax pale yellow with blackish markings; shiny and weakly iridescent under some angles of illumination; rubbed. *Eyes*: generally as in ♂. *Clypeus*: fringed by long white hairs below anterior median eyes. *Chelicerae*: yellow-brown, shiny with scattered yellow-brown hairs along inner margins; promargin with three teeth, retromargin with six or seven (Fig. 8E). *Maxillae and labium*: as in ♂. *Sternum* (Fig. 8B): as in ♂. *Coxae*: pale yellow. *Abdomen*:

whitish grey with sooty markings; rubbed. *Legs*: moderately long and slender with numerous spines; light yellow-brown grading to yellow-brown distally. Spination of legs I: metatarsi v 2-2-0, p 1-0-1, d 0-2-2, r 1-0-1; tibiae v 2-3-2, p 1-1-0, d 0-1-0, r 1-1-0; patellae p 0-1-0, r 0-1-0; femora d 0-2-4. *Epigyne* (Fig. 8D): clothed in fine golden hairs.

Dimensions (mm): total length 5·76; carapace length 2·2, breadth 1·84, height 1·4; abdomen length 3·36; eyes, anterior row 1·76, middle row 1·53, posterior row 1·74; quadrangle length 1·29 (58 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 14 : 8 : 5·5 : 8; AL–PM–PL :: 8–9·5; AM CL :: 14 : 2.

VARIATION. A paratype ♂ measures 4·48 mm total length, 2·12 mm carapace length. The carapace is clothed in scattered pale amber hairs above, while the abdomen has poorly defined blackish markings, as in ♀, with fine recumbent pale golden hairs and scattered stiff brownish ones.

DISTRIBUTION. Malaysia: Sarawak.

MATERIAL EXAMINED. **Sarawak,** Gunung Mulu National Park, (*F. R. Wanless,* R.G.S./ Sarawak Government Expedition): holotype ♂, paratype ♀, Melinau Gorge, on limestone cliff, 9.v.1978. (BMNH. 1981.11.5.1–2); paratype ♂, Gunung Mulu, summit helicopter pad, on shrubs, 2275 m. 29.v.1978 (BMNH. 1981.11.5.3).

Mintonia mackiei sp. n.
(Fig. 9A–D)

DIGNOSIS. By the elongate bifid retrolateral tibial apophysis (Fig. 9C, D).

Female. Unknown.

Male holotype, in good condition. *Carapace* (Fig. 9A): yellow-brown faintly tinged black; clothed in recumbent light and dark brownish hairs with central white haired stripe from level of posterior median eyes to posterior thoracic margin. *Eyes*: with blackish surrounds except anterior medians; fringed by light brownish hairs with whitish ones around lower rims of anteriors. *Clypeus*: clothed in long white hairs. *Chelicerae*: pale yellow-brown with black markings; shiny with scattered stiff brownish hairs; promargin with three teeth, retromargin with four or five. *Maxillae and labium*: whitish yellow faintly tinged black. *Stenum*: pale yellow tinged black, somewhat stippled; shiny with scattered light amber hairs. *Coxae*: pale yellow-brown; shiny. *Abdomen*: clothed above in recumbent dark brown hairs with two white haired stripes followed by series of five white spots posteriorly; venter greyish yellow thinly covered in brown and whitish hairs; spinnerets pale yellow-brown with basal segments of anteriors tinged black. *Legs*: moderately long and slender with numerous spines and minute light brownish spot (femoral organ) on under side of femora I; yellow-brown, clothed in dark brown hairs, forming stripes on femora, with somewhat incomplete bands of whitish hairs on patellae, tibiae and metatarsi. Spination of legs I: metatarsi v 2-0-0, p 1-1-1, d 0-2-1, r 1-1-2; tibiae v 2-2-2, p 2-0-1, d 1-1-0, r 2-0-1; patellae p 0-1-0, r 0-1-0; femora d 0-1-4, p 0-0-1. *Palp* (Fig. 9C, D): lobe M_2 evidently lacking; tegular furrow a lightly sclerotised groove (arrowed, Fig. 9C); tibia deeply excavated.

Dimensions (mm): total length 3·68; carapace length 1·66, breadth 1·44, height 1·0; abdomen length 1·88; eyes, anterior row 1·44, middle row 1·19, posterior row 1·32; quadrangle length 1·04 (62 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 11 : 7 : 5 : 6·6; AL–PM–PL :: 6–7; AM : CL :: 11 : 3·5.

DISTRIBUTION. Indonesia: Kalimantan.

MATERIAL EXAMINED. **Borneo,** Kalimantan, rig 8, on road between Balikpapan and Samboja, holotype ♂, 6.iii.1976, (*R. Thomson*) (BMNH. 1981.11.5.4).

REMARKS. The prongs of the retrolateral tibial apophysis may each possess a distal opening,

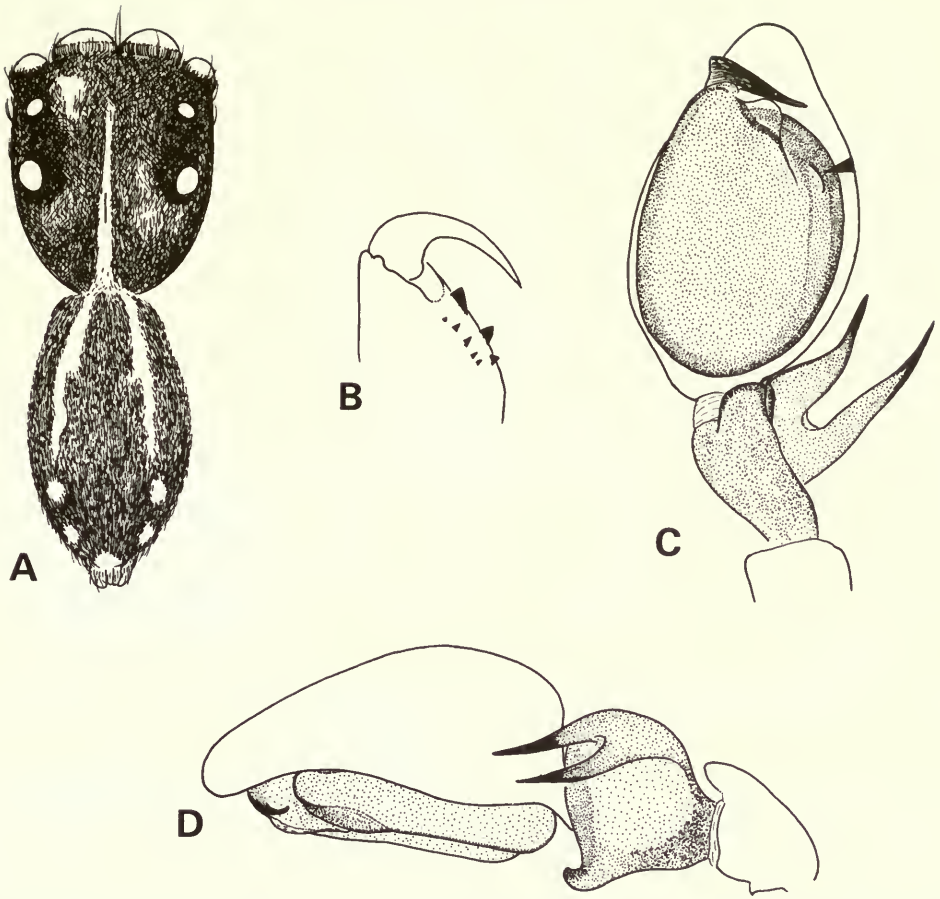

Fig. 9 *Mintonia mackiei* sp. n., holotype ♂: A, dorsal; B, cheliceral teeth, inner view; C, palp, ventral; D, palp, retrolateral.

for the posterior prong (Fig. 9C) contains an amorphous substance for part of its length, while the other appears to contain a duct, possibly an artifact, under certain angles of illumination.

ETYMOLOGY. Named in honour of Mr D. W. Mackie, Stockport, Cheshire.

Mintonia nubilis sp. n
(Fig. 10A–F)

DIAGNOSIS. By the thin median epigynal ridge (Fig. 10F).

Male. Unknown, but see remarks below.

Female holotype, in fair condition. *Carapace* (Fig. 10A, B): dark brown suffused and mottled with black; irregularly clothed in light amber hairs (rubbed) with fine black hairs on thoracic sides; on thoracic margins from coxae I to IV a narrow band of short white hairs; also on central part of thorax a few scattered white hairs possibly remains of a median stripe. *Eyes*: with black surrounds except anterior medians; generally fringed in amber hairs, but with white and amber ones on rims of anterior row. *Clypeus*: margin clothed in whitish and scattered black hairs with ill-defined oblique whitish bands converging between anterior median eyes; elsewhere thinly covered in light amber hairs. *Chelicerae*: yellow-brown suffused with some black; thinly clothed in scattered light brown hairs; promargin with three teeth, retro-

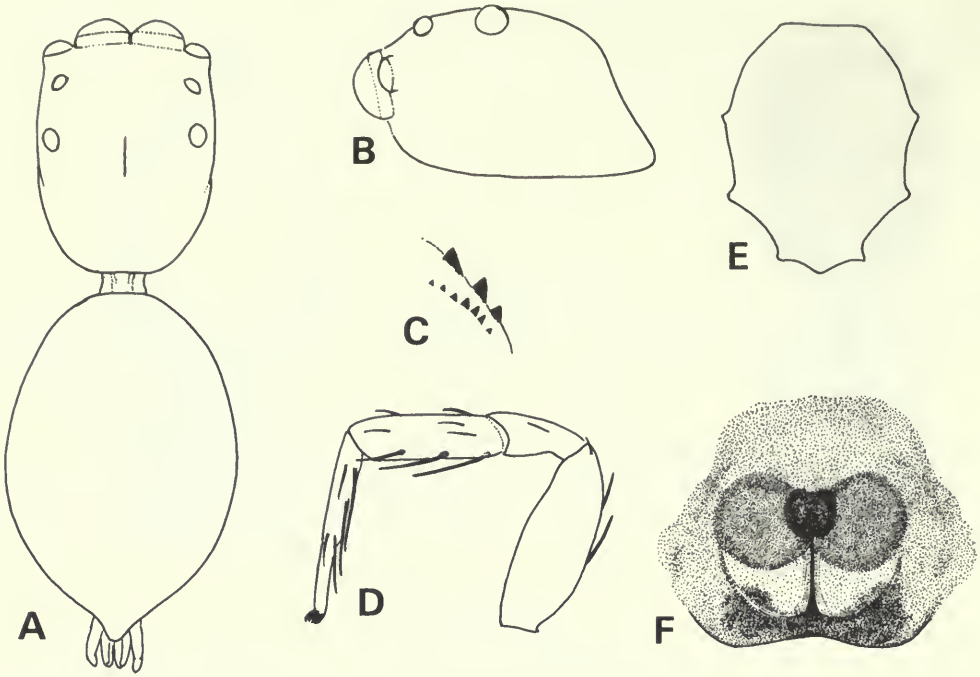

Fig. 10 *Mintonia nubilis* sp. n., holotype ♀: A, dorsal; B, carapace, lateral; C, cheliceral teeth, inner view; D, leg I; E, sternum; F, epigyne.

margin with seven (Fig. 10C). *Maxillae and labium*: yellow-brown lightly tinged with some black. *Sternum* (Fig. 10E): yellow-brown lightly suffused black; thinly clothed in fine pale brown hairs. *Coxae*: yellow-brown with sooty markings on lateral sides. *Abdomen*: mostly rubbed, original pattern lost; generally light greyish yellow with vague black markings; partly clothed in light brown and blackish hairs; spinnerets light yellow-brown tinged black on outer sides of anteriors and medians. *Legs*: moderately long and slender with numerous spines; generally light to dark yellow-brown with vague sooty markings except for femora I which are heavily suffused black and weakly iridescent violet under some angles of illumination. Spination of legs I: metatarsi v 2-2-0, p 1-0-1, d 0-2-2, r 1-0-1; tibiae v 2-2-2, r 1-0-1, d 1-1-0, p 2-0-1; patellae p 0-1-0, r 0-1-0; femora d 0-2-4. *Palps*: yellow-brown lightly tinged with some black; clothed in whitish and dark brown hairs. *Epigyne* (Fig. 10F): clothed in fine whitish hairs.

Dimensions (mm): total length c. 4·8 (pedicel stretched); carapace length 1·88; breadth 1·52, height 1·23; abdomen length 2·72; eyes, anterior row 1·44, middle row 1·26, posterior row 1·43; quadrangle length 1·0 (53 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 11 : 7 : 5 : 6; AL–PM–PL :: 6–8; AM : CL :: 11 : 4.

DISTRIBUTION. Indonesia: Kalimantan.

MATERIAL EXAMINED. **Borneo:** Kalimantan, Sepaku (Balikpapan), from a leaf, 16. vii. 1979, holotype ♀, (*P. R. Deeleman*) (RNH, Leiden).

REMARKS. This species represented by a single female may be conspecific with *M. mackiei,* known only from the male, but the presence of narrow white marginal bands on the carapace, lacking in *mackiei,* suggests that they are separate taxa and are treated as such for the present.

Mintonia protuberans sp. n.
(Fig. 11A–F)

DIAGNOSIS. Readily by the prong arising from the base of the embolus (Fig. 11C, arrowed).

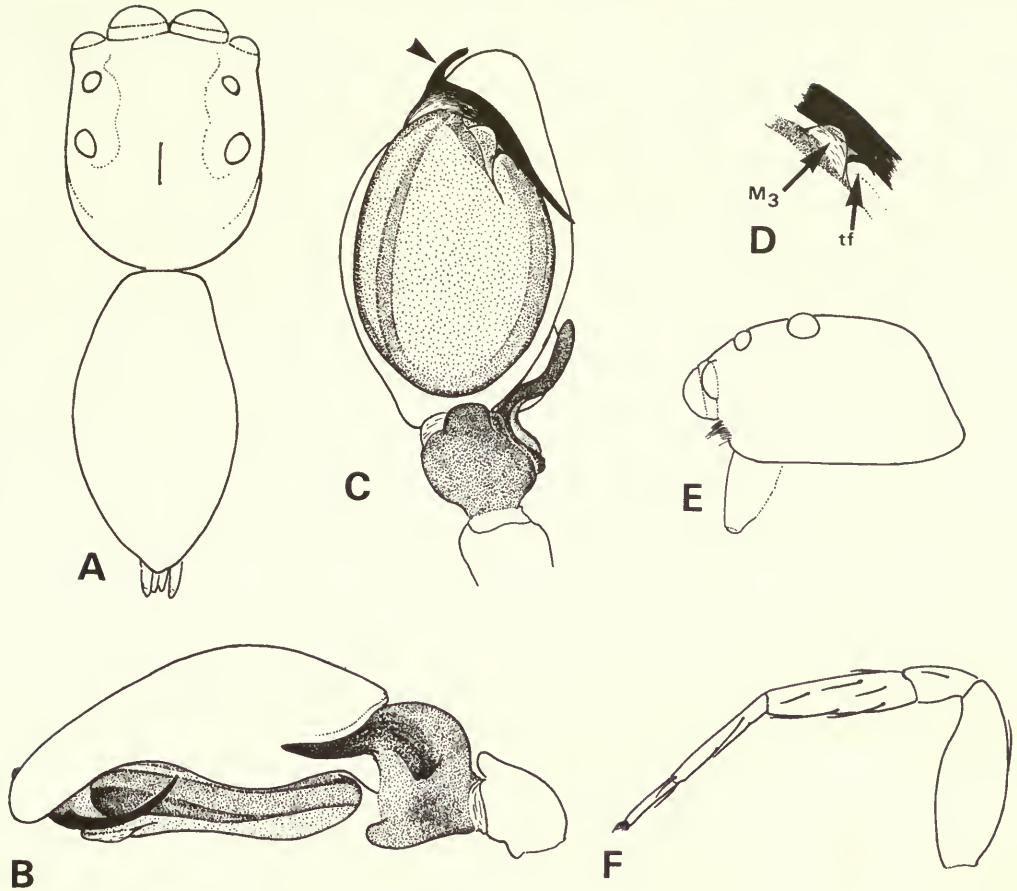

Fig. 11 *Mintonia protuberans* sp. n., holotype ♂: A, dorsal; B, palp, retrolateral; C, palp, ventral; D, region M_3; E, carapace, lateral; F, leg I. Abbreviation: tf, tegular furrow.

Female. Unknown.

Male holotype, in poor condition. *Carapace* (Fig. 11A, E): yellow-brown lightly tinged black with vague sooty markings on thoracic part; weakly iridescent green under some angles of illumination; irregularly clothed in recumbent light amber and whitish hairs (mostly rubbed) with thin marginal fringe of short white hairs. *Eyes*: with blackish surrounds; fringed by light amber hairs with whitish ones around lower rims of anterior medians and anterior laterals. *Clypeus*: white haired. *Chelicerae*: distally amber otherwise dark brown with sooty markings; promargin with three teeth retromargin with six. *Maxillae*: yellow-brown suffused with some black. *Labium*: yellow-brown tinged black with paler distal margin. *Sternum*: yellow-brown tinged black. *Coxae*: yellow-brown. *Abdomen*: amber faintly tinged black grading to greyish white posteriorly; rubbed, but with scattered patches of amber, and whitish hairs; spinnerets yellow-brown tinged black. *Legs*: broken, some missing; generally dark brownish with lighter annuli; sparsely clothed in whitish hairs on metatarsi and tibiae; femoral organ apparently lacking; spines strong and numerous. Spination of legs I: metatarsi v 2-1-1, p 1-1-1, d 0-2-2, r 1-1-1; tibiae v 2-2-2, p 0-1-1, d 1-1-0, r 0-1-1; patellae p 0-1-0, r 0-1-0; femora p 0-0-1, d 0-2-4. *Palp* (Fig. 11B–D): generally dark brown with whitish hairs on femora and patella and brownish ones on tibia and cymbium; the lobe M_2 is lacking.

Dimensions (mm): total length 4·6; carapace length 2·12, breadth 1·72, height 1·28; abdomen length 2·52; eyes, anterior row 1·64, middle row 1·36, posterior row 1·52; quadrangle length 1·10 (51 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 12·5 : 8 : 5 : 7; AL–PM–PL : 7–8; AM : CL :: 12·5 : c.3·5.

DISTRIBUTION. Singapore.

MATERIAL EXAMINED. **Singapore:** holotype ♂, (*H. N. Ridley*) (BMNH. 1981.11.5.6).

Mintonia breviramus sp. n.
(Fig. 12A–E)

DIAGNOSIS. By the stumpy embolus and form of the retrolateral tibial apophysis in males (Fig. 12D, E), and the curved tubular rim of the epigynal opening in females (Fig. 12B).

Male holotype, in fair condition. *Carapace*: orange-brown tinged black in eye region; irregularly clothed in brown, and whitish hairs, mostly rubbed. *Eyes*: with blackish surrounds except anterior medians; fringed by whitish hairs appearing light amber under some angles of illumination. *Clypeus*: tinged black with lateral sooty markings; thinly covered in light brown hairs. *Chelicerae*: orange-brown with sooty markings; shiny with scattered light brown hairs; promargin with three teeth, retromargin with six. *Maxillae, labium, sternum and coxae*: light yellow-brown. *Abdomen*: generally pale yellow-brown with black spots near bases of anterior spinnerets; mostly rubbed, otherwise clothed in short shiny light golden and amber hairs. *Legs*: moderately long and slender with numerous spines and slightly raised pore (femoral organ) on underside of femora I; generally light yellow-brown. Spination of

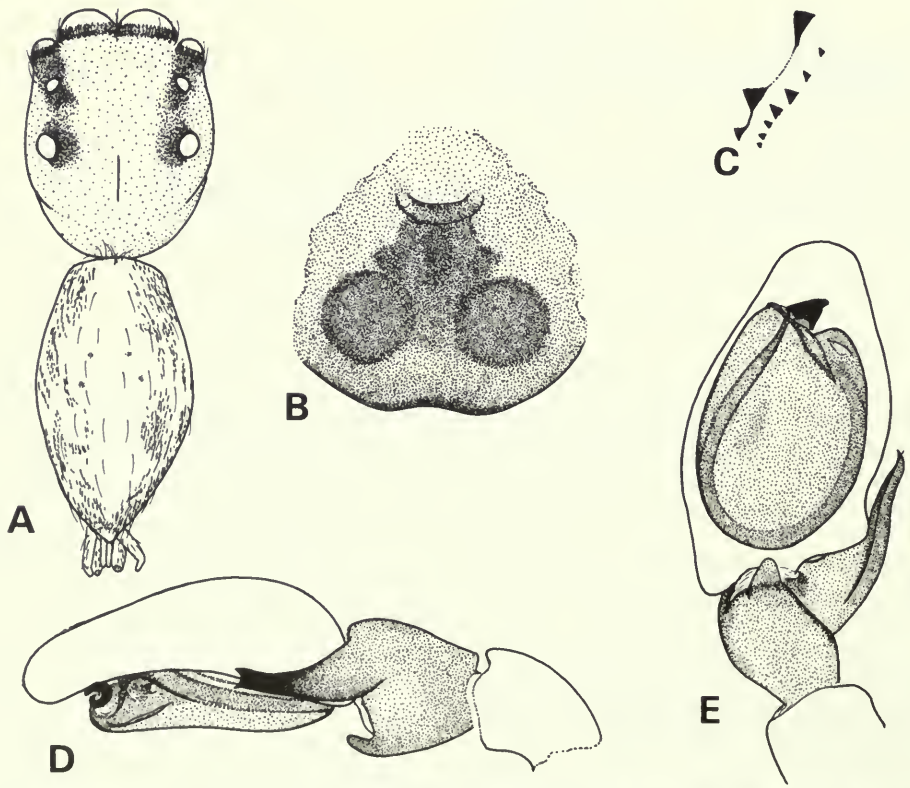

Fig. 12 *Mintonia breviramus* sp. n., holotype ♂: D, palp, retrolateral; E, palp, ventral. Paratype ♀: A, dorsal; B, epigyne; C, cheliceral teeth, inner view.

legs I: metatarsi v 2-2-0, p 1-0-1, d 0-1-2, r 1-1-1; tibiae v 2-2-2, p 1-0-1, d 1-1-0, r 1-0-1; patellae p 0-1-0, r 0-1-0; femora d 0-2-3, p 0-0-1. *Palp* (Fig. 12D, E): distal haematodochal region present as a minute lobe (M_2) lying over the embolic base.

Dimensions (mm): total length 3·72; carapace length 1·72, breadth 1·45, height 1·12; abdomen length 1·8; eyes, anterior row 1·36, middle row 1·26, posterior row 1·4; quadrangle length 1·0 (58 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 11 : 6 : 4 : 6; AL–PM–PL :: 6–6·5; AM : CL :: 11 : 3.

Female paratype. Slightly faded, but otherwise in good condition. *Carapace* (Fig. 12A): yellow-brown with vague creamy markings; clothed in recumbent pale amber, and whitish hairs. *Eyes*: with black surrounds except anterior medians; fringed by creamy white hairs. *Clypeus*: clothed in creamy white hairs. *Chelicerae*: yellow-brown with scattered light amber hairs; promargin with three teeth, retromargin with seven (Fig. 12C). *Maxillae, labium, sternum and coxae*: pale yellow. *Abdomen*: pale yellow; dorsum clothed in recumbent pale yellow hairs with mottled pattern of pale amber ones on sides; spinnerets pale yellow-brown. *Legs*: moderately long and slender with numerous spines; yellow-brown grading to amber distally especially on first pair. Spination of legs I: metatarsi v 2-0-0, p 1-1-1, d 0-2-2, r 1-1-1; tibiae v 2-2-2, p 1-1-0, d 0-1-1, r 1-1-0; patellae p 0-1-0, r 0-1-0; femora d 0-2-4. *Epigyne* (Fig. 12B): reddish orange clothed in fine testaceous hairs.

Dimensions (mm): total length 5·44; carapace length 2·48, breadth 2·04, height 1·56; abdomen length 2·8; eyes, anterior row 1·84, middle row 1·56, posterior row 1·8; quadrangle length 1·4 (56 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 14 : 8·5 : 6 : 9; AL–PM–PL :: 7·5–11; AM : CL :: 11 : 4.

VARIATION. A paratype ♂ measures 3·6 mm total length, 1·64 mm carapace length.

DISTRIBUTION. Malaysia: Sarawak.

MATERIAL EXAMINED. **Sarawak,** Baram District, Mt. Dulit, (Oxford University Sarawak Expedition): holotype ♂, (BMNH. 1952.9.8.1); paratype ♂, (SM. Kuching); paratype ♀, Koyan Forest, beaten from trees, xi.1932 (BMNH. 1952.9.8.234).

Mintonia melinauensis sp. n.
(Fig. 13A–D)

DIAGNOSIS. By the heavy inward curving embolus and the form of the retrolateral tibial apophysis (Fig. 13B, C).

Female. Unknown.

Male holotype, in fair condition. *Carapace* (Fig. 13A, D): dark brown suffused and mottled black; clothed in short amber hairs with thin white haired stripe on thoracic part and narrow white haired marginal bands extending from level of coxae II to IV. *Eyes*: with dark surrounds; fringed by amber hairs. *Clypeus*: thinly clothed in amber and blackish hairs. *Chelicerae*: yellow-brown suffused and mottled black with scattered long black hairs; promargin with three teeth, retromargin with six. *Maxillae and labium*: pale yellow-brown tinged black. *Sternum*: yellow-brown tinged black; shiny, thinly covered in light brownish hairs. *Abdomen*: yellow-brown tinged and mottled black; irregularly clothed in shiny amber hairs (?rubbed); spinnerets pale yellow tinged black. *Legs*: first pair missing, others generally yellow-brown to orange-brown tinged with some black forming vague annuli on legs III–IV; spines strong and numerous. *Palps* (Fig. 13B, C): apophysal opening indicated by an arrow (Fig. 13C).

Dimensions (mm): total length 3·85; carapace length 1·84, breadth 1·48, height 1·24; abdomen length 1·88; eyes, anterior row 1·38, middle row 1·2, posterior row 1·32; quadrangle length 0·96 (52 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 11 : 6·5 : 4 : 6; AL–PM–PL :: 6–6·5; AM : CL :: 11 : 5.

DISTRIBUTION. Malaysia; Sarawak.

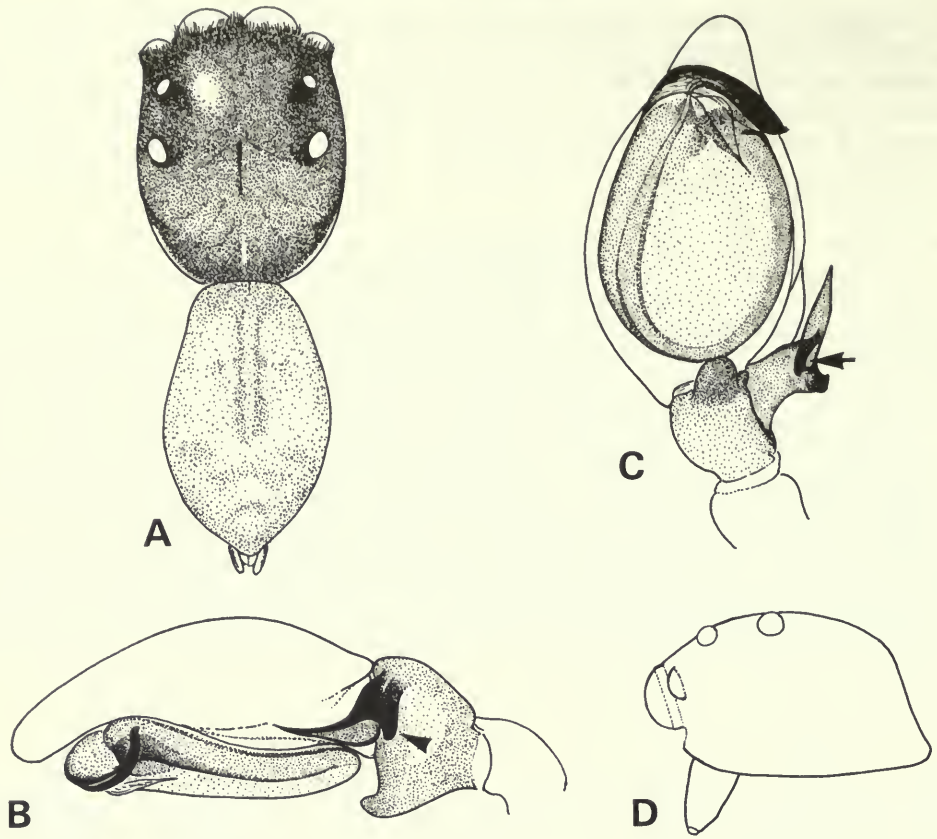

Fig. 13 *Mintonia melinauensis* sp. n., holotype ♂: A, dorsal; B, palp, retrolateral; C, palp, ventral; D, carapace, lateral.

MATERIAL EXAMINED. **Sarawak:** Gunung Mulu National Park, R.G.S./Sarawak Government Expedition, holotype ♂, Melinau Gorge, 21.vi.1978 (*F. R. Wanless*) (BMNH. 1981.11.5.5).

Mintonia ramipalpis (Thorell) comb. n.
(Figs 14A–I; 15A–C: 34A, B; 35E, F; 36F)

Cocalus ramipalpis Thorell, 1892: 353, 475, ♂, ♀. LECTOTYPE ♂, PARALECTOTYPE ♀ (here designated) Sumatra, (UM, Oxford) [examined]. Thorell, 1890: 165. Wanless, 1981: 202 [belongs in *Boethus*].

Phaeacius ramipalpis: Simon, 1901: 406–408. Roewer, 1954: 935. Bonnet, 1958: 3494.

DIAGNOSIS. Readily by the structure of the male palps (Fig. 14B, F) and female epigyne (Fig. 15A–C).

Male from Sarawak, in good condition. *Carapace* (Fig. 14A, C): yellow-brown, shiny; eye region and upper part of thorax covered in amber hairs with patchy covering of dark brownish hairs on thoracic sides; on lateral sides patches of cuticle apparently free of hairs or clothed in fine weakly iridescent whitish hairs, a similar vague band extends from foveal region to posterior margin. *Eyes*: with blackish surrounds; posteriors fringed by amber hairs, anteriors by amber and whitish ones. *Clypeus*: clothed in white hairs, dense and long on margins near chelicerae becoming shorter on sides and extending posteriorly to level of coxae I–II. *Chelicerae*: pale yellow; basal half clothed in long white hairs; promargin with three teeth, retromargin with seven. *Maxillae and labium*: pale yellow lightly tinged with some

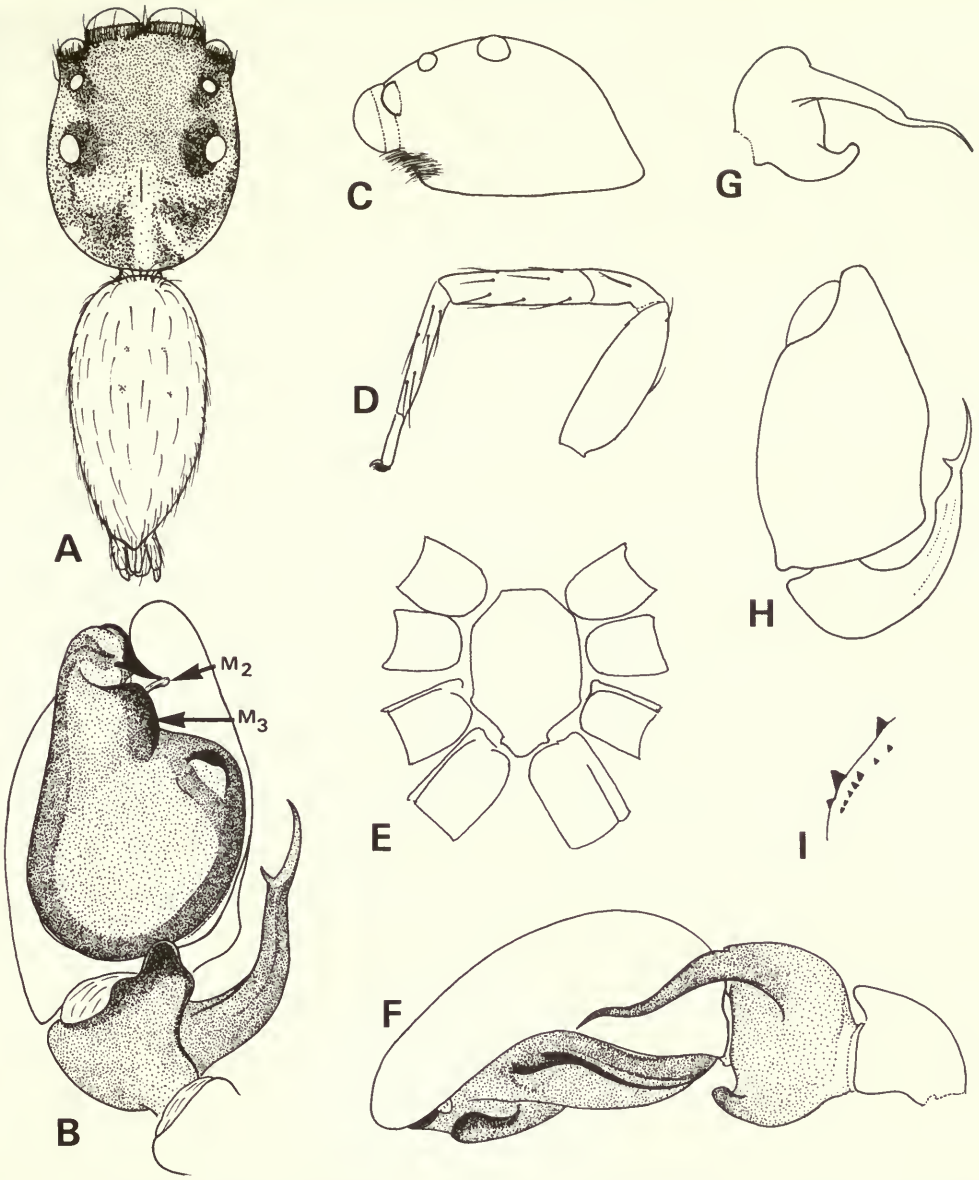

Fig. 14 *Mintonia ramipalpis* (Thorell), ♂: A, dorsal; B, palp, ventral; C, carapace, lateral; D, leg I; E, sternum and coxae; F, palp, retrolateral; G, palpal tibia, retrolateral; H, cymbium and retrolateral tibial apophysis, dorsal; I, cheliceral teeth, inner view.

grey. *Sternum* (Fig. 14E): pale yellow with fine scattered hairs. *Coxae*: pale yellow. *Abdomen*: pale yellow with two pairs of obscure impressed spots; clothed in pale and dark amber hairs with scattered long greyish ones. *Legs*: moderately long and slender with numerous moderately robust spines and minute light amber spot (femoral organ) on under side of femora I; pale yellow to yellow-brown. Spination of legs I: metatarsi v 2-2-2-, p 0-0-1, d 0-2-2, r 0-0-1; tibiae v 2-2-2, p 1-1-0, d 1-1-0, r 1-1-0; patellae p 0-1-0, r 0-1-0; femora p 0-0-1, d 0-2-3. *Palp* (Fig. 14B, F–H): hirsute with tufts of long white hairs on inside of femora, patellae and tibiae. The lobe M_2 is obscured by hairs and is not as conspicuous as shown in Fig. 14B.

Dimensions (mm): total length c. 5·6; carapace length 2·24, breadth 1·76, height 1·4; abdomen length 2·32; eyes, anterior row 1·6, middle row 1·34, posterior row 1·56; quadrangle length 1·2 (53 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 13 : 7·5 : 5 : 7·5; AL–PM–PL :: 7–9; AM : CL :: 13 : c. 4·5.

Female from Sumatra, in fair condition. *Carapace*: yellowish brown with dark amber eye region; clothed in whitish hairs with scattered patches of pale amber ones; mostly rubbed. *Eyes*: with blackish surrounds except anterior medians; fringed by whitish hairs. *Chelicerae*: orange-brown, shiny; clothed sparsely in amber hairs; teeth as in ♂. *Maxillae*: pale orange-brown grading to whitish yellow on inner distal margin. *Labium*: pale orange-brown tipped whitish yellow. *Sternum*: pale yellow with darker margins. *Abdomen*: pale dirty yellow-brown, clothed in recumbent whitish hairs with patches of amber hairs forming a somewhat speckled pattern, also as in ♂ a scattering of long stiff hairs; venter greyish yellow with series of minute indistinct spots. *Legs*: moderately long and slightly more robust than in ♂ with numerous spines; pale to dark yellow-brown with vague annuli on posterior legs, also darker patches on femora IV. Spination of legs I: metatarsi v 2-0-0, p 1-1-1, d 0-2-2, r 1-1-1; tibiae v 2-2-2, p 1-1-0, r 1-0-0; patellae p 0-1-0, r 0-1-0; femora d 0-2-4. *Epigyne* (Fig. 15A–C): clothed in fine whitish hairs.

Dimensions (mm): total length c. 7·5; carapace length 3·12, breadth 2·36, height 1·68; abdomen length 4·36; eyes, anterior row 2·04, middle row 1·96, posterior row 2·0; quadrangle length 1·54 (49 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 16·5 : 9·5 : 6 : 9·5; AL–PM–PL :: 9·5–11; AM : CL :: 16·5 : c. 4.

VARIATION. ♂ total length varies from 4·52 to 5·6 mm, carapace length 2·08–2·32 mm (4 specimens); paralectotype ♀ measures c. 6·8 mm total length, 2·92 mm carapace length. Most of the specimens examined were rubbed and generally pale yellow-brown with only vague markings. In males the retrolateral tibial apophysis varies slightly in thickness and the basal protuberance of the cymbium varies in development being a little more pronounced in some individuals. In the female from Sumatra the T-shaped epigynal marking is indistinct and the spermathecae are set closer together.

DISTRIBUTION. Indonesia: Java, Sumatra; Malaysia: Sarawak.

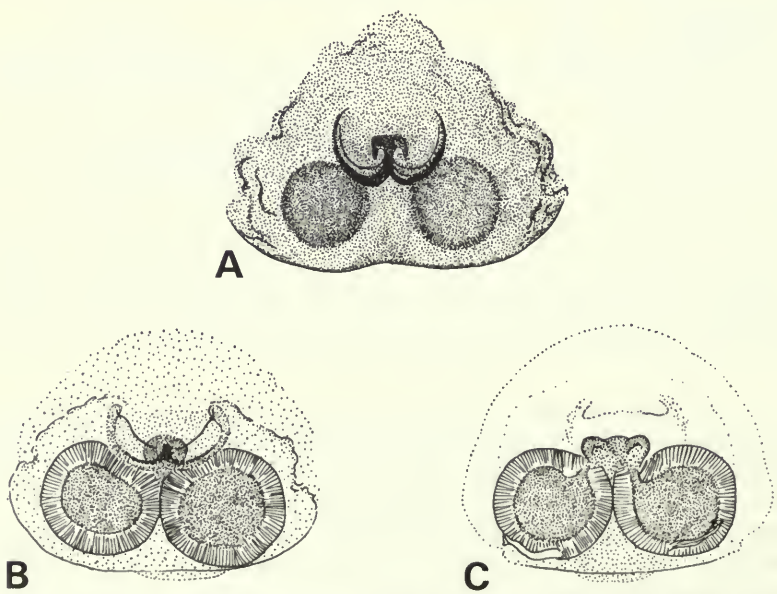

Fig. 15 *Mintonia ramipalpis* (Thorell), paralectotype ♀: A, epigyne. Another specimen: C, vulva, outer view; B, vulva, inner view.

MATERIAL EXAMINED. **Java**: 1♀, no other data (BMNH). **Sarawak,** Gunung Mulu National Park, R.G.S./Sarawak Government Expedition: 1♂, alluvial forest, from tree trunks environs of base camp, 2.v.1978 (*F. R. Wanless*); 1♂, mixed dipterocarp forest, brushed off mossy trunks and rocks (*J. Marshall*) (BMNH); 1♂, mixed dipterocarp forest, pitfall trap 28.iii.1978 (*M. Collins*) (Sarawak Museum, Kuching). **Sumatra:** Lectotype ♂, paralectotype ♀, (UM, Oxford).

Genus *GELOTIA* Thorell

Gelotia Thorell, 1890: 164. Type species *Gelotia frenata* Thorell, by subsequent designation (Thorell, 1892: 344). Thorell, 1892: 345. Simon, 1901: 412, 413. Waterhouse, 1902: 146. Petrunkevitch, 1928: 184. Neave, 1939, II: 452. Roewer, 1954: 957. Bonnet, 1957: 1986. Prószyński, 1968: 12, 13; 1971: 410.

Policha Thorell, 1892: 351. Type species *Gelotia* (?)*bimaculata* Thorell, by original designation. Simon, 1901: 412, 413. Petrunkevitch, 1928: 185. Neave, 1940, III: 844. Roewer, 1954: 957. Bonnet, 1958: 3745. Prószyński, 1968: 12, 13 [=*Gelotia*]; 1971: 461.

[*Polichus* Waterhouse, 1902: 298, lapsus calami].

Codeta Simon, 1900: 33. Type species *Codeta argenteolimbata* Simon, by original designation and monotypy. Simon, 1901: 411–413. Waterhouse, 1902: 80. Petrunkevitch, 1928: 184. Neave, 1939, I: 783. Roewer, 1954: 957. Bonnet, 1956: 1176. Prószyński, 1971: 391. Wanless, 1981: 254. **Syn. n.**

DEFINITION. Spiders of medium size, i.e. total length between 4·0 and 8·0 mm. Sexual dimorphism evidently not marked; patterns generally inconspicuous.

Carapace: moderately high, longer than broad, widest at about level between coxae II–III; fovea moderately long, sulciform, apex behind or near centre of posterior lateral eyes; moderately hairy (i.e. in species known from unrubbed specimens) sometimes with white marginal bands. *Eyes*: with relatively weak to moderately strong lenses, set on low tubercles; anteriors contiguous or subcontiguous with apices weakly procurved or weakly recurved in frontal view; anterior laterals more than half diameter of anterior medians; posterior medians small or relatively large, positioned midway or slightly closer to and on or just outside optical axis of anterior laterals; posterior laterals as large or slightly smaller than anterior laterals and positioned just inside lateral margins of carapace when viewed from above; posterior ocular quadrangle broader than long, wider behind; entire quadrangle between 43 and 57 per cent of carapace length. *Clypeus*: low to moderately high. *Chelicerae*: moderately robust, parallel or slightly diverging and slightly inclined anteriorly; fang moderately robust and curved; promargin with three teeth, retromargin with four or five. *Maxillae*: moderately long, more or less parallel with rounded outer distal margins. *Labium*: as long or slightly longer than broad and about half maxillae length. *Sternum*: more or less elongate scutiform. *Abdomen*: elongate ovoid to long and narrow; patterns generally inconspicuous, but largely unknown as most species represented by rubbed specimens; spinnerets moderately long, posteriors moderately slender and as long or slightly longer than robust anteriors, medians shorter and more slender than anteriors; *Legs*: moderately long and slender with numerous moderately strong spines; ventral tibial fringes rarely present; males sometimes with minute tubercle (femoral organ) on underside of femora I; claws pectinate, tufts present, scopulae absent, but tarsi I and apices of metatarsi I with minute setae (c.f. *Portia*). *Female palps*: moderately long and slender with distal claw. *Male palps*: relatively large, complex and interspecifically fairly distinct with strongly developed interlocking protuberances; femora robust, rarely possessing large ventral apophysis bearing minute peg-like spines; patellae with moderate to strong anterodorsal tubercle; tibiae with anterodorsal tubercle, obtuse ventral apophysis and cap-shaped (i.e. in ventral view) retrolateral apophysis which sometimes bears a backward pointing syringe-like process; cymbium with distal scopulae, and sometimes pronounced basal excavations and tubercles; embolus short and stout to long and slender, generally curving inwards towards alveolus; distal haematodocha largely obscured with elements M_1 and M_2 usually bearing lobes (Fig. 16A–C), the latter (M_2) sometimes not readily separated from tegular ledge M_3; tegulum generally subovoid with peripheral seminal duct, an open or irregular furrow which

may extend around retrolateral margin, and lobe-like process bearing the distal haematodocha, embolus and curtain-like membrane—the tegular ledge M_3; median haematodocha, subtegulum and basal haematodocha not examined. *Epigynes*: of various forms; median longitudinal ridge sometimes present; copulatory openings positioned anteriorly, occasionally obscured by black hood-like surrounds; introductory ducts short and bent or looped, opening into spermathecae, often large, bearing fertilisation ducts on posterior margin; in one species, opposite the epigyne and on other side of epigastric furrow a curved sclerotised fold.

DIAGNOSIS. Males readily by cap-like appearance of the retrolateral tibial apophyses in ventral aspect (e.g. Fig. 20I), in one species there is an additional backward pointing process (Fig. 21D, I). Females with more difficulty by details of the epigyne which is usually characterised by the presence of a thin median ridge (Fig. 17C).

Key to species of *Gelotia*

Males (those of ***frenata*** are unknown)

1 Posterior median eyes relatively small (PM : PL :: 1 : 4) 2
– Posterior median eyes relatively large (PM : PL :: 3 : 4) 3
2 Palpal femora with large ventral apophysis bearing minute peg-like spines (Fig. 18C) (Singapore) . . . ***argenteolimbata*** Simon (p. 174)
– Palpal femora lacking a ventral apophysis; distal haematodocha with large lobe-like process M_2, Figs 17D; 35C,D) (Borneo, Sumatra) . . . . . ***bimaculata*** Thorell (p. 172)
3 Palpal RTA with backward pointing syringe-like process (Fig. 21D, I) (Malaysia) . . . ***syringopalpis*** sp. n. (p. 178)
– Palpal RTA without a backward pointing process 4
4 Embolus long and slender (Fig. 20I) (Sulawesi) . . . . . ***salax*** (Thorell) (p. 176)
– Embolus short and robust (Fig. 19F) (New Britain) . . . . . ***robusta*** sp. n. (p. 174)

Females (those of ***argenteolimbata, robusta*** and ***salax*** are unknown)

1 Posterior median eyes relatively small (PM : PL :: 1 : 4); epigyne with median longitudinal ridge (Figs 16F; 17C) 2
– Posterior median eyes relatively large (PM : PL :: 3 : 4); epigyne without median longitudinal ridge (Fig. 21C) (Malaysia) . . . . . ***syringopalpis*** sp. n. (p. 178)
2 Legs I with ventral fringe of hairs on tibiae (Sumatra) . . . . . ***frenata*** Thorell (p. 170)
– Legs I lacking ventral fringe of hairs on tibiae (Borneo, Sumatra) ***bimaculata*** Thorell (p. 172)

Gelotia frenata Thorell
(Fig. 16D–F)

Gelotia frenata Thorell, 1890: 345, ♀. Holotype ♀, Sumatra (MCSN, Genova) [examined]. Thorell, 1892: 345, 475. Simon, 1901: 412, 413. Petrunkevitch, 1928: 184. Roewer, 1954: 857. Bonnet, 1957: 1896. Prószyński, 1968: 13; 1971: 410.

DIAGNOSIS. By the presence of ventral fringes on the underside of the tibiae of legs I.

Male. Unknown, but *G. argenteolimbata* possibly belongs here.

Female holotype, in poor condition. *Carapace* (Fig. 16D): brownish grey with yellow-brown eye region; lateral sides densely clothed, apart from rubbed patches, in whitish hairs with indistinct marginal bands of light brownish ones, eye region rubbed, but dorsum of thoracic part with scattered whitish hairs posteriorly, becoming fine, clear and weakly iridescent towards foveal region. *Eyes*: with black surrounds except anterior medians; anteriors fringed by whitish hairs. *Clypeus*: edged in whitish hairs. *Chelicerae*: amber faintly tinged black; shiny; clothed basally in whitish hairs mixed with overlaying clypeal ones, with scattered long amber hairs along inner sides; promargin with three teeth, retromargin with four. *Maxillae and labium*: light yellowish brown with greyish brown markings. *Sternum*: yellowish

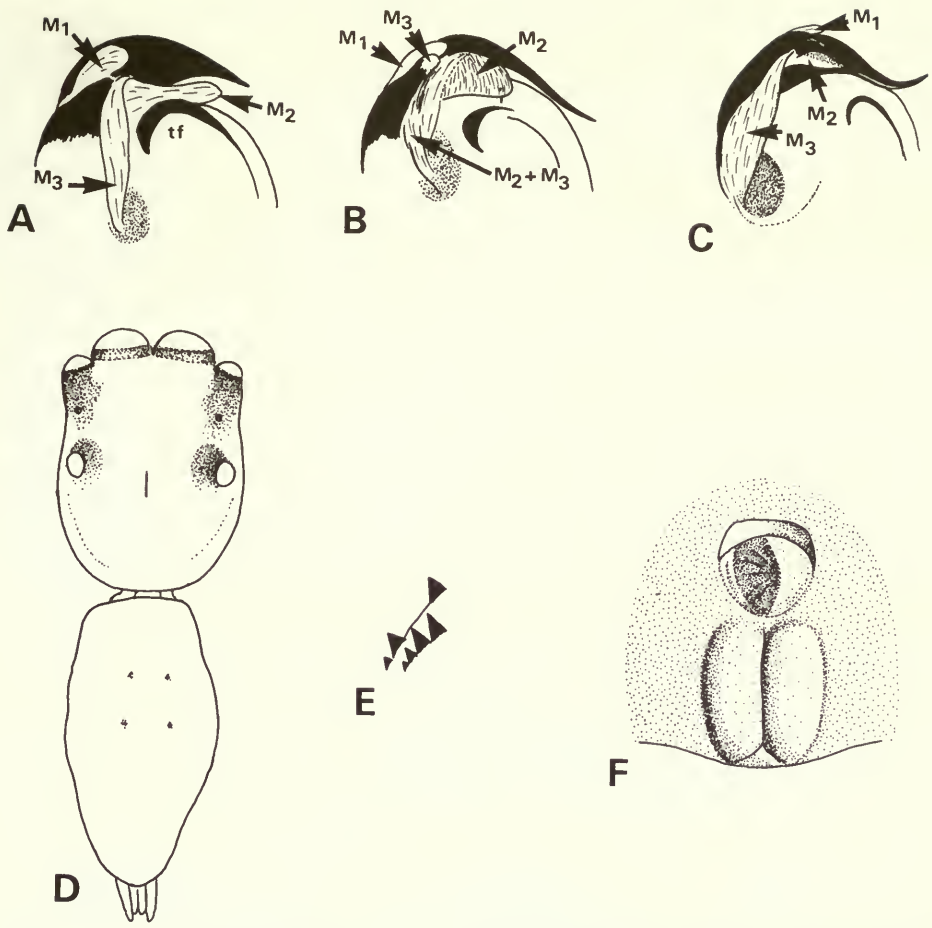

Fig. 16 (A–C) *Gelotia* spp. showing elements of distal haematodocha and tegular ledge, schematic: A, *G. argenteolimbata* (Simon); B, *G. bimaculata* Thorell, note M_2 and M_3 partly fused; C, *G. robusta* sp. n. (D–F) *Gelotia frenata* Thorell, holotype ♀: D, dorsal; E, cheliceral teeth, inner view; F, epigyne, after Prószyński (1968). Abbreviation: tf, tegular furrow.

brown with slightly darker margins; shiny, clothed in pale greyish hairs. *Coxae*: yellowish brown; shiny. *Abdomen*: dirty pale yellow-brown with vague greyish markings; mostly rubbed, but with patches of fine whitish/iridescent, and dark amber hairs on dorsum and sides with amber, and long greyish hairs ventrally; spinnerets yellowish brown tinged black. *Legs*: long and slender, generally yellowish brown with fringes of stout greyish yellow hairs on underside of tibiae, patellae and apex of femora of legs I and apex of femora of legs IV; spines strong and numerous. Spination of legs I: metatarsi v 2-0-2, p 1-0-0, d 2-1-2, r 1-1-0; tibiae v 2-2-2, p 1-0-1, d 1-1-0, r 1-1-0; patellae p 0-1-0, r 0-1-0; femora p 0-0-1, d 0-2-3, r 0-1-0. *Palp*: pale yellow-brown with darker tarsi; clothed in whitish hairs. *Epigyne* (Fig. 16F): see remarks below.

Dimensions (mm): total length 6·36; carapace length 2·84, breadth 2·34, height c. 1·76; abdomen length 3·56; eyes, anterior row 2·24, middle row 1·8, posterior row 2·11; quadrangle length 1·64 (57 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 18·5 : 10 : 2·2 : 10; AL–PM–PL :: 12 : 11·5; AM : CL :: 18·5 : 5.

DISTRIBUTION. Indonesia: Sumatra.

MATERIAL EXAMINED. **Sumatra,** Sungei Bulu, holotype ♀, ix.1878 (*O. Beccari*) (MCSN, Genova).

REMARKS. Prószyński (1968) gave a good description of this specimen, but cleared the epigyne which is now preserved in canada balsam on a microscope slide. Its original appearance (Fig. 16F) is therefore redrawn from Prószyński's text Figure 5.

Gelotia bimaculata Thorell
(Figs 17A–J; 30E–F; 33A, B; 35C, D)

Gelotia (?) bimaculata Thorell, 1892: 348, ♀, juvenile ♀. LECTOTYPE ♀ (here designated) Borneo, (MCSN, Genova) [examined]. Prószyński, 1968: 12–20 [restored to *Gelotia*].

Policha bimaculata (Thorell). Thorell, 1892: 351 [assigned to *Policha*]. Simon, 1901: 413. Petrunkevitch, 1928: 185. Roewer, 1954: 957. Bonnet, 1958: 3745. Prószyński, 1968: 12–20; 1971: 461.

Codeta bouchardi Simon, 1903: 305, ♂. LECTOTYPE ♂ (here designated) Sumatra (MNHN, Paris). Roewer, 1954: 957. Bonnet, 1956: 1176. Prószyński, 1971: 391. **Syn. n.**

DIAGNOSIS. Similar to *G. argenteolimbata* known only from the male and *G. frenata* known only from the female, by having relatively small posterior median eyes. Differs from *argenteolimbata* by lacking a robust apophysis on the underside of the palpal femora, and from *frenata* by the absence of ventral fringes on the tibiae of the first pair of legs.

Male from Sarawak, in good condition. *Carapace* (Fig. 17A, F): brownish orange covered in recumbent black lanceolate hairs shining iridescent violet under some angles of illumination; also from level of coxae II to IV a marginal band of short white hairs, and on thoracic slope a central narrow white haired band with streaks of whitish hairs on either side. *Eyes*: with black surrounds; fringed by blackish hairs. *Clypeus*: with scattered long stiff black hairs and numerous short black ones forming a more or less distinct marginal fringe. *Chelicerae*: dark amber with sooty markings; shiny; thinly clothed in stiff black hairs; promargin with three teeth, retromargin with four. *Maxillae and labium* (Fig. 17A): yellow-brown lightly suffused black. *Sternum*: yellow-brown lightly suffused black; thinly clothed in stiff brownish hairs. *Abdomen*: raised and somewhat square fronted anteriorly; generally greyish; covered in recumbent black/iridescent violet lanceolate hairs interspersed with clear hairs forming a vague pattern of chevrons, also a conspicuous white haired spot practically covering the anal tubercle and on lateral sides longitudinal bands of whitish hairs; spinnerets pale yellow-brown tinged black except for creamy white medians; clothed in blackish hairs. *Legs*: long and slender with numerous spines and minute tubercle (femoral organ) on underside of femora I (Figs 17G; 30E, F); generally yellow-brown; clothed in recumbent black lanceolate hairs particularly on metatarsi, tibiae, patellae and upper surfaces of femora; also on tibiae IV a patch of whitish hairs. Spination of legs I: metatarsi v 2-0-2, p 1-1-0, d 0-0-2, r 1-1-0; tibiae v 2-2-2, p 1-1-0, d 1-1-0, r 1-1-0; patellae p 0-1-0, r 0-1-0, femora p 0-0-1, d 0-2-3, r 0-1-1. *Palp* (Figs. 17D, H; 33A, B): clothed in black hairs with whitish hairs on tibiae and patellae.

Dimensions (mm): total length 7·2; carapace length 3·36, breadth 2·54, height 1·88; abdomen length 4·0; eyes, anterior row 2·28, middle row 1·96, posterior row 2·24; quadrangle length 1·8 (53 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 19 : 10·5 : 3 : 11; AL–PM–PL :: 12–14; AM : CL :: 10·5 : 5·5.

Female from Sarawak, in poor condition. General habitus similar to male. *Carapace*: brownish orange with an iridescent sheen and scattered covering of fine black hairs interspersed with patches of more robust whitish ones especially on thoracic part. *Eyes*: similar to male, but fringed by whitish, and dirty pale amber hairs. *Clypeus*: clothed in scattered whitish hairs. *Chelicerae*: dark orange-brown lightly tinged black with coppery iridescent sheen under some angles of illumination; thinly clothed in mixed short whitish and long black hairs; promargin with three teeth, retromargin with four; fang with basal third a little swollen. *Maxillae and*

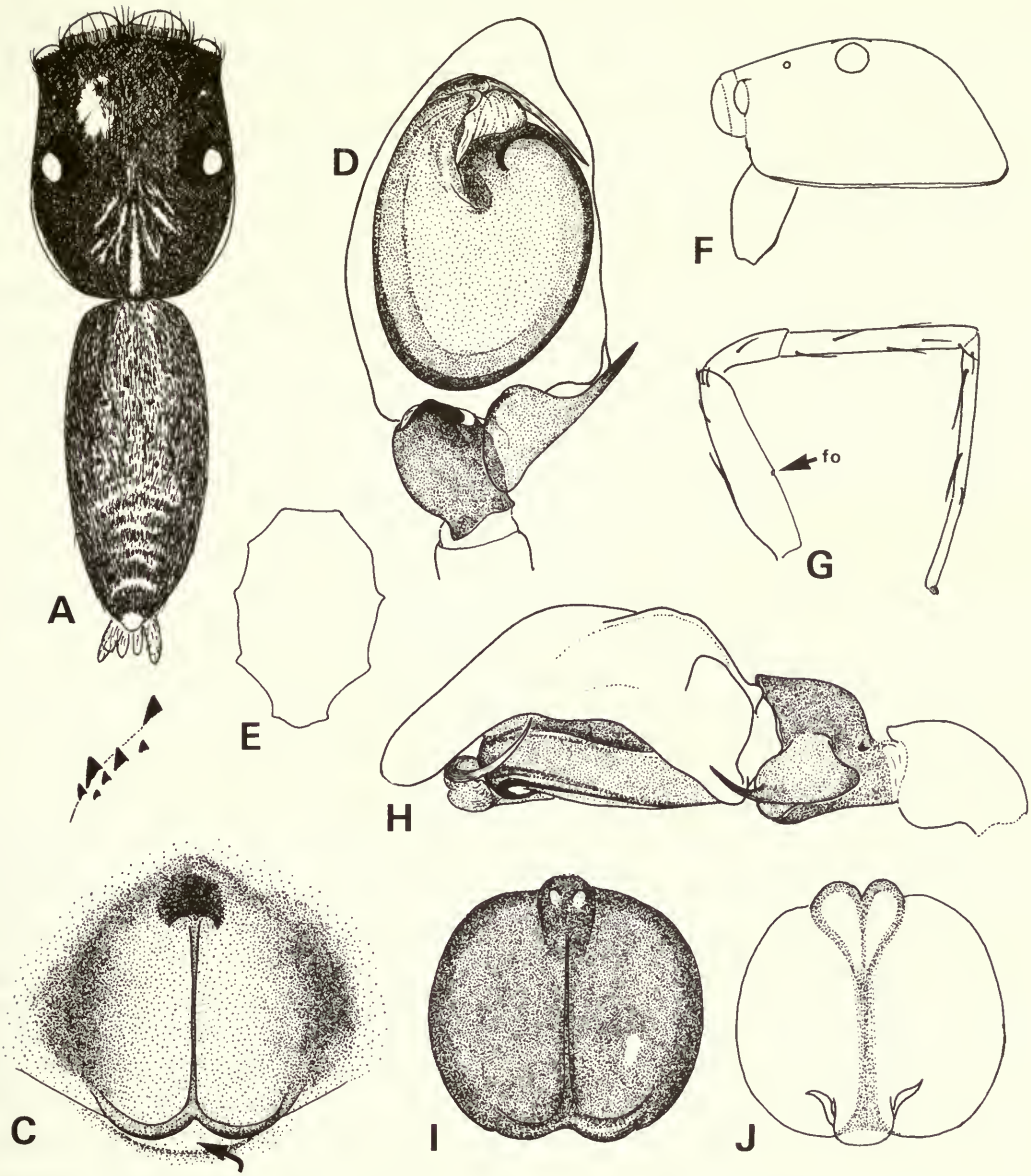

Fig. 17 *Gelotia bimaculata* Thorell, ♂: A, dorsal; B, cheliceral teeth, inner view; D, palp, ventral; E, sternum; F, carapace, lateral; G, leg I; H, palp, retrolateral. ♀: C, epigyne; I, vulva, outer view; J, vulva, inner view. Abbreviation: fo, femoral organ.

labium: orange-brown tinged black with inner distal margin of maxillae and labial tip yellowish. *Sternum*: orange-brown tinged black; shiny; sparsely clothed in stiff black hairs. *Abdomen*: grey-black somewhat speckled with four apodemal spots; badly rubbed, but with patches of brown-black and whitish hairs posteriorly. *Legs*: moderately long and slender with numerous spines; tarsi I yellow-brown, legs otherwise orange-brown suffused and mottled with some black. Spination of legs I: metatarsi v 2-0-2, tibiae v 2-2-2, p 1-0-0; patellae p 0-1-0; femora p 0-0-1, d 0-1-4. *Palp*: dark brownish orange suffused and mottled black, iridescent violet under some angles of illumination especially tarsi and tibiae. *Epigyne* (Fig. 17C, I, J): relatively large with a median ridge and dark copulatory openings; also, opposite the posterior margin on the other side of the epigastric furrow a curved sclerotised fold.

Dimensions (m): total length c. 7·7; carapace length 3·08, breadth 2·4, height 1·92; abdomen length 4·72; eyes, anterior row 2·24, middle row 1·88, posterior row 2·12; quadrangle length 1·76 (57 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 18 : 10 : 3 : 10; AL–PM–PL :: 12·5 : 3·5; AM : CL :: 18 : 4.

VARIATION. Males vary from 5·68–8·16 mm total length, 2·84–3·96 mm carapace length, four specimens. Another female, lectotype of *G. bimaculata,* measures 8·32 mm total length, 3·8 mm carapace length.

DISTRIBUTION. Indonesia: Kalimantan; Sumatra. Malaysia: Sarawak.

MATERIAL EXAMINED. **Kalimantan**: Makunjung, 1♂, 21.iv. 1976 (*J. R. Thomson*) (BMNH). **Sarawak**: lectotype ♀ [of *Gelotia bimaculata*) (*O. Beccari & G. Doria*) (MCSN, Genova); Gunung Mulu National Park, R.G.S./Sarawak Government Expedition: alluvial forest, environs of base camp 1♀, iv. 1978 (*P. Chapman*); Hidden Valley, mixed dipterocarp forest-helicopter landing pad, 1♂, iv. 1978 (*P. Chapman*); Melinau Gorge, evirons of camp 5, 1♂, 18.v.1978 (*F. R. Wanless*) (BMNH). **Sumatra**: Forêt du Nirou, Palembang Province, lectotype ♂ [of *Codeta bouchardi*] (*M. J. Bouchard*) (MNHN, Paris, 22187).

Gelotia argenteolimbata (Simon) Comb. n.
(Fig. 18A–F)

Codeta argenteo-limbata Simon, 1900: 33, ♂. LECTOTYPE ♂ (here designated) Singapore (MNHN, Paris) [examined].
Codeta argenteolimbata Simon. Simon, 1901: 411–413. Petrunkevitch, 1928: 184. Roewer, 1954: 957. Bonnet, 1956: 1176. Prószyński, 1971: 391.

DIAGNOSIS. By the presence of a robust apophysis on the underside of the palpal femora (Fig. 18C).

Female. Unknown, but possibly belongs with *G. frenata.*

Male lectotype, in fair condition. *Carapace* (Fig. 18A, B): orange-brown lightly tinged and mottled black with paler eye region; rubbed, but short recumbent hairs forming rather patchy submarginal white bands from level of coxae I to IV. *Eyes*: with black surrounds except anterior medians; fringed by some whitish hairs; lenses of anteriors damaged. *Clypeus*: probably rubbed, but with several fine hairs and stout bristles. *Chelicerae*: pale yellow-brown with sooty markings; promargin with three teeth, retromargin with four. *Maxillae and labium*: pale yellow-brown lightly tinged with some black. *Sternum*: pale yellow-brown faintly tinged black; shiny. *Abdomen*: pale yellow-brown with faint sooty markings; clothed in fine recumbent iridescent setae; spinnerets whitish yellow. *Legs*: long and slender with numerous spines; femoral organs lacking; generally pale yellow-brown with faint markings on femora, patella and tibiae of legs I. Spination of legs I: metatarsi v 2-0-1, p 1-1-1, r 1-1-1; tibiae v 2-2-2, p 1-1-0, d 1-1-1, r 1-1-0, patellae p 0-1-0, r 0-1-0; femora p 0-0-1, d 1-1-3. *Palp* (Fig. 18C, D): the retrolateral tibial apophysis has an amorphous interior suggesting the presence of a distal opening.

Dimensions (mm): total length 5·04; carapace length 2·32, breadth 1·8, height 1·4; abdomen length 2·8; eyes, anterior row 1·78, middle row 1·52, posterior row 1·76; quadrangle length 1·32 (56 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 15 : 8·5 : 2 : 8; AL–PM–PL :: 10–10; AM : CL :: 15 : c. 6.

DISTRIBUTION. Singapore.

MATERIAL EXAMINED. **Singapore:** lectotype ♂, (*E. Simon*) (MNHN, Paris, 12820).

Gelotia robusta sp. n.
(Fig. 19A–F)

DIAGNOSIS. Comparable with *G. salax* by having large posterior median eyes, but easily distinguished by the short robust embolus (Fig. 19F).

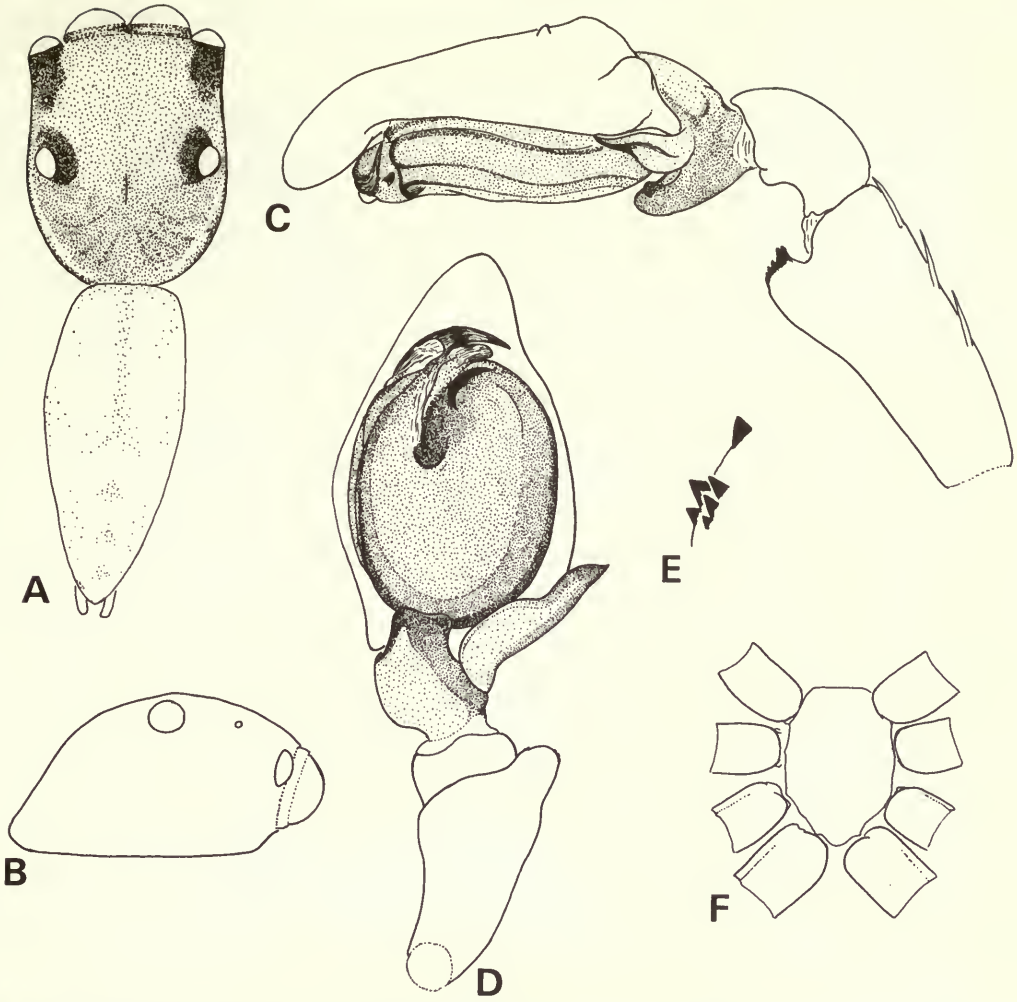

Fig. 18 *Gelotia argenteolimbata* (Simon), lectotype ♂: A, dorsal; B, carapace, lateral; C, palp, retrolateral; D, palp, ventral; E, cheliceral teeth, inner view; F, sternum and coxae.

Female. Unknown.

Male holotype, in fair condition. *Carapace* (Fig. 19A, B): orange-brown lightly mottled black on sides; clothed in short whitish and pale amber hairs with short black hairs on mottling. *Eyes*: with black surrounds except anterior medians; fringed by whitish and pale amber hairs. *Clypeus*: clothed in long pale amber hairs. *Chelicerae*: generally yellow-brown to orange-brown tinged with some black; clothed in whitish and pale amber hairs with scattered stiff black ones; promargin with three teeth, retromargin with five. *Maxillae and labium*: yellow-brown tinged black with inner margins of maxillae and labial tip paler. *Sternum* (Fig. 19C): yellow-brown suffused with black; clothed in grey-black hairs with whitish ones around anterior margins. *Coxae*: yellow-brown with black on inner sides of coxae I. *Abdomen*: rubbed; generally yellow-brown with blackish markings on lateral sides and irregular covering of recumbent pale amber and black hairs; also, posteriorly on one side a sparse tuft of white hairs; ventrally a tapering sooty band. *Legs*: moderately long and slender with numerous spines; femoral organ evidently lacking; geneally yellow-brown with vague sooty annuli on metatarsi and tibiae of legs III–IV. Spination of legs I: metatarsi v 3-0-0, p 1-1-0, d 0-2-2,

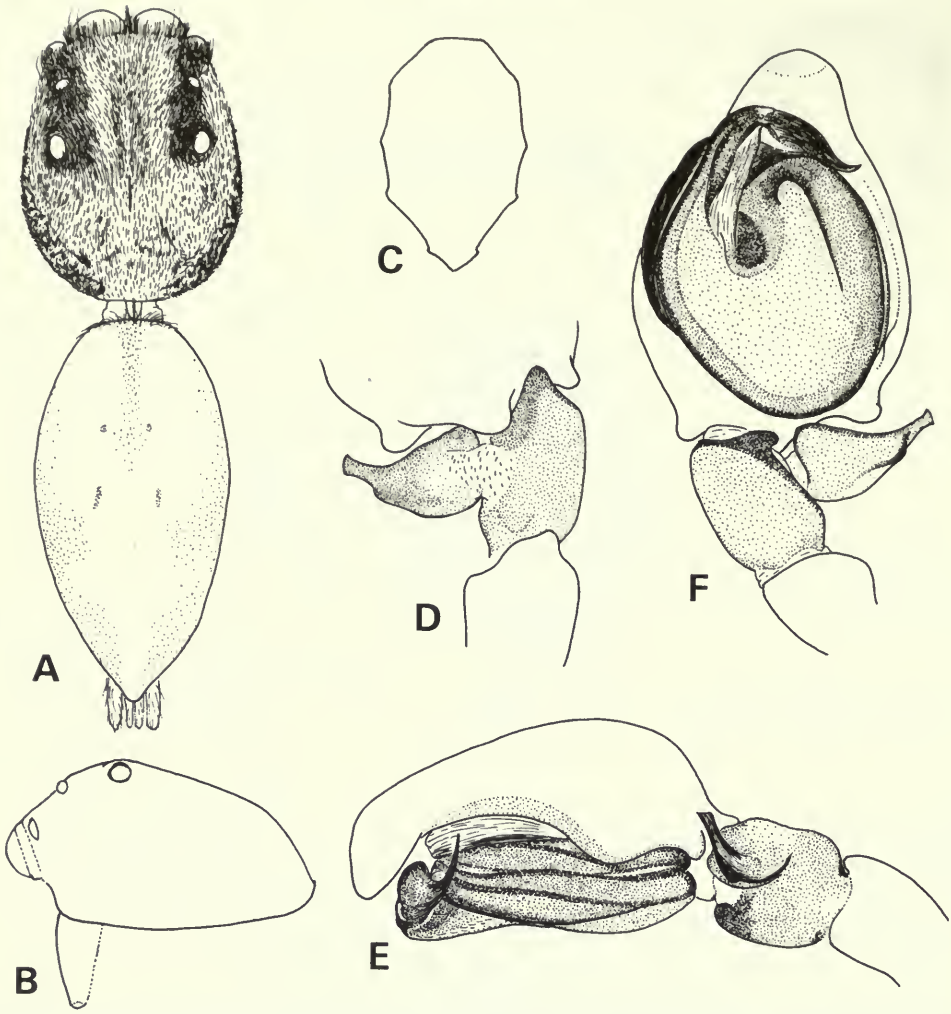

Fig. 19 *Gelotia robusta* sp. n., holotype ♂: A, dorsal; B, carapace, lateral; C, sternum; D, retrolateral tibial apophysis and locking mechanism, dorsal; E, palp, retrolateral; F, palp, ventral.

r 2-0-1; tibiae v 2-2-2, p 0-1-2, d 1-0-2, r 0-1-1; patellae p 0-1-0, r 0-1-0; femora d 0-2-4. *Palp* (Fig. 19D–F): the short embolus curves inwards towards the alveolus.

Dimensions (mm): total length c. 7·2 (pedicel stretched); carapace length 3·04, breadth 2·4, height 1·84; abdomen length 3·92; eyes, anterior row 1·84, middle row 1·6, posterior row 1·82; quadrangle length 1·32 (43 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 14·5 : 7·5 : 5·5 : 7·5; AL–PM–PL :: 9–11; AM : CL :: 14·5 : 8.

DISTRIBUTION. Papua New Guinea: East New Britain.

MATERIAL EXAMINED. **Papua New Guinea,** Keravat, Gazelle Peninsula, East New Britain, holotype ♂, pyrethrum knockdown sample, Wairiki cocoa plantation, 13.vi.1979 (*Stewart Smith,* 021–024) (MCZ, Harvard).

Gelotia salax (Thorell) comb. n.
(Fig. 20A–I)

Cocalus salax Thorell, 1877: 594, ♂ only [see remarks]. LECTOTYPE ♂ (here designated) Celebes

(MCSN, Genova) [examined]. Thorell, 1892: 352, 475. Simon, 1901: 407. Roewer, 1952: 934. Bonnet, 1956: 1174. Prószyński, 1971: 391.

REMARKS. The immature female described by Thorell (1877: 597) belongs in *Cocalus* Koch.

DIAGNOSIS. Readily by the long slender embolus and the form of the retrolateral tibial apophysis.

Female. Unknown.

Male lectotype, in poor condition. *Carapace* (Fig. 20A, B, D): dark amber, weakly iridescent under some angles of illumination; irregularly clothed in short recumbent white hairs (rubbed). *Eyes*: with brown-black surrounds; fringed by whitish hairs. *Clypeus*: clothed in light amber hairs. *Chelicerae*: dark amber with sooty markings grading to yellowish orange

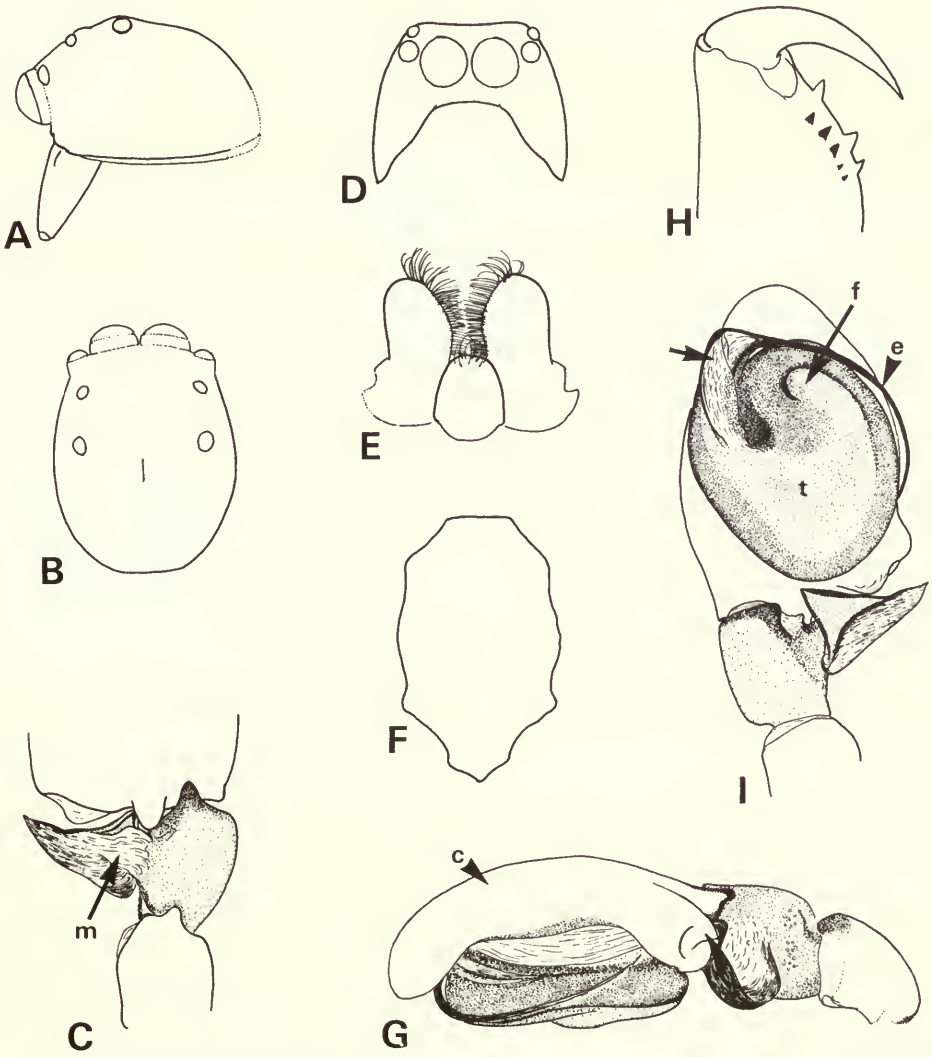

Fig. 20 *Gelotia salax* (Thorell, lectotype ♂: A, carapace lateral; B, carapace, dorsal; C, retrolateral tibial apophysis and locking mechanism, dorsal; D, facies; E, maxillae and labium; F, sternum; G, palp, retrolateral; H, cheliceral teeth, inner view; I, palp, ventral. Abbreviations: c, cymbium; e, embolus; f, tegular furrow; m, membraneous attachment; t, tegulum.

distally; sparsely clothed (?rubbed) in long pale amber and short dull whitish hairs; promargin with three teeth, retromargin with four. *Maxillae*: light brown with whitish inner margins. *Labium*: brown tipped whitish with sclerotised patches basally. *Sternum*: (Fig. 20F): light brown with amber margins. *Abdomen*: damaged; apparently elongate ovoid; pale grey with white and pale amber hairs; pattern indiscernible. *Legs*: generally yellow-brown to light amber. Spination of legs I: metatarsi v 2-1-0, p 1-1-0, d 0-2-2, r 1-2-0; tibiae v 2-2-2, p 1-1-0, d 2-2-0, r 1-0-0; patellae p 0-1-0, r 0-1-0; femora d 1-1-4. *Palp* (Fig. 20C, G, I): the amorphous region 'm' seems to form the only means of attachment between the tibia and retrolateral apophysis.

Dimensions (mm): total length c. 7·4; carapace length 3·4; breadth 2·68, height 1·96; abdomen length c. 4·0; eyes, anterior row 2·16, middle row 1·92, posterior row 2·06; quadrangle length 1·6 (47 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 17 : 9 : 6 : 8; AL–PM–PL :: 10–13; AM : CL :: 17 : 6.

DISTRIBUTION. Indonesia: Sulawesi.

MATERIAL EXAMINED. **Sulawesi,** Kandari lectotype ♂, (*Dott. O. Beccari,* 1874) (MCSN, Genova).

Gelotia syringopalpis sp. n.
(Fig. 21A–I)

DIAGNOSIS. The most derived species in the genus easily recognised by the syringe-like process of the retrolateral tibial apophysis in males (Fig. 21D, I), and by the appearance of the epigyne in females (Fig. 21C).

Male holotype, in fair condition. *Carapace*: light orange-brown with paler thoracic stripe and vague marginal bands; eye region clothed in shining hairs with fine dark amber hairs elsewhere except for whitish ones on stripe and marginal bands. *Eyes*: with black surrounds except anterior medians; fringed by whitish, and pale golden hairs. *Clypeus*: with black markings; thinly clothed in long whitish hairs. *Chelicerae*: yellow-brown with sooty markings and scattered fine yellowish hairs; promargin with three teeth, retromargin with five. *Maxillae and labium*: yellow-brown lightly tinged grey with fine scattered hairs. *Sternum*: pale yellow-brown, margins slightly darker; sparsely clothed in light brown hairs. *Coxae*: yellow-brown with scattered light brownish hairs. *Abdomen*: whitish yellow with vague sooty markings posteriorly; sparsely clothed in stiff brownish hairs with fine recumbent shiny hairs dorsally and scanty patches of amber ones on sides; spinnerets yellow-brown heavily tinged black. *Legs* (Fig. 12E): moderately long and slender with numerous spines and minute tubercle (femoral organ) on underside of femora I; pale to dark yellow-brown with blackish tarsi I. Spination of legs I: metatarsi v 2-1-0, p 0-1-0, d 2-1-2, r 0-1-0; tibiae v 2-2-2, p 1-0-1, d 1-1-0, r 1-0-1; patellae p 0-1-0, r 0-1-0; femora p 0-0-1, d 0-2-3, r 0-1-0. *Palp* (Fig. 21D, I): the profile of the retrolateral tibial apophysis in ventral aspect is like that of other *Gelotia* species in spite of the syringe-like process, which has a whitish exudate blocking the opening in this particular specimen.

Dimensions (mm): total length 4·4; carapace length 2·14, breadth 1·68, height 1·32; abdomen length 2·28; eyes, anterior row 1·64, middle row 1·56, posterior row 1·64; quadrangle length 1·2 (56 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 13 : 7·8 : 5 : 8; AL–PM–PL :: 8 : 7·5; AM : CL :: 13 : 4.

Female paratype, in good condition. Habitus similar to ♂ except for the following. *Carapace* (Fig. 21A, B): lacking marginal bands. *Clypeus*: thinly clothed in fine light brown, and whitish hairs with several stout bristles. *Chelicerae*: more bulbous than in ♂; yellow-brown, shiny with scattered stout brown hairs. *Maxillae, labium, sternum and coxae*: as in ♂, but scattered hairs darker and more conspicuous. *Abdomen*: yellow-brown, with scattered bristles and dense covering of short dark brownish hairs with pale golden ones forming a vague median stripe; spinnerets yellow-brown suffused black. *Legs*: generally as in ♂, but tarsi I yellow-

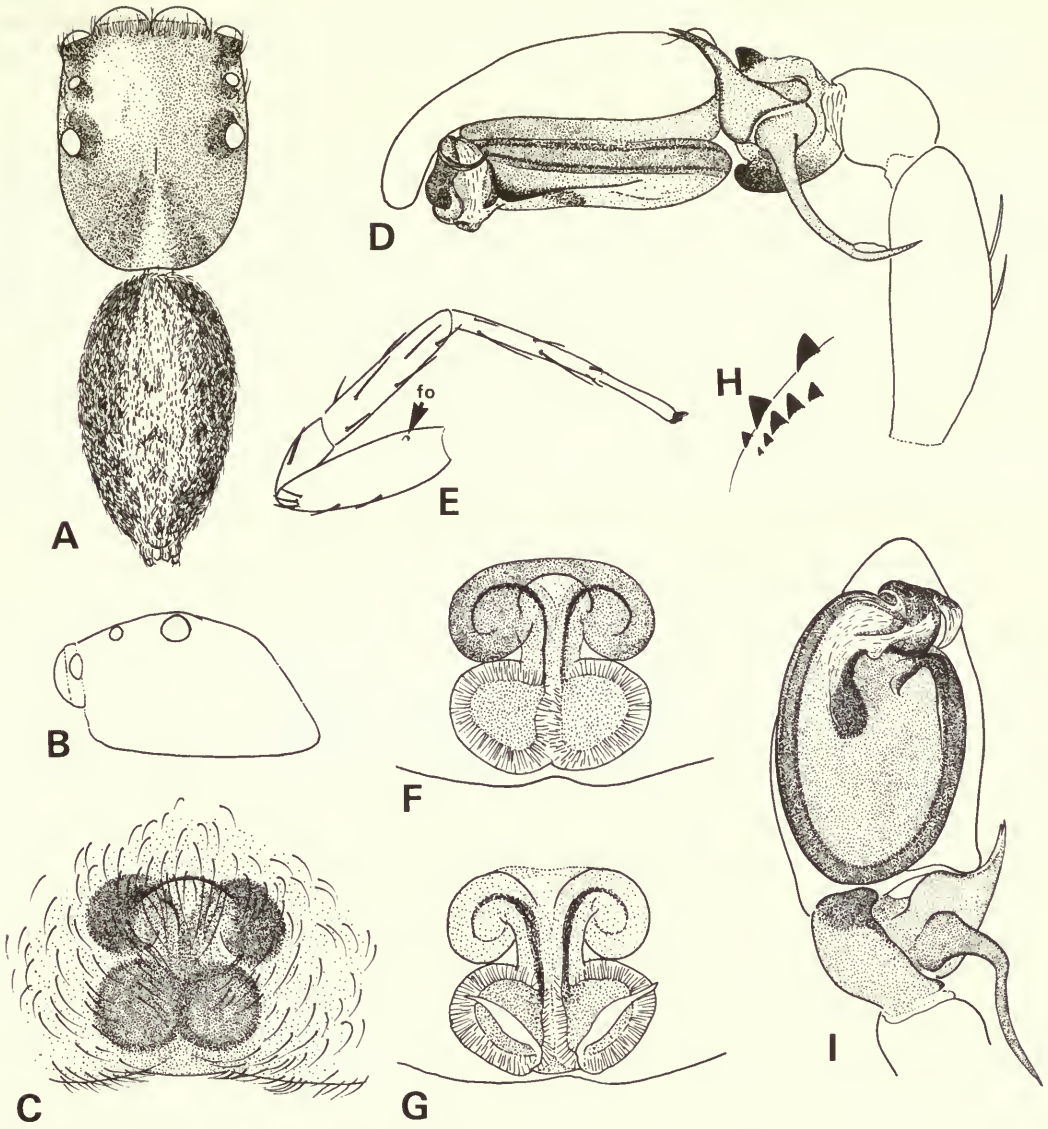

Fig. 21 *Gelotia syringopalpus* sp. n., holotype ♂: D, palp, retrolateral; E, leg I; I, palp, ventral. Paratype ♀: A, dorsal; B, carapace, lateral; C, epigyne; F, vulva, outer view; G, vulva, inner view; H, cheliceral teeth, inner view. Abbreviation: fo, femoral organ.

brown. Spination of legs I: metatarsi v 2-1-1; tibiae v 2-2-2, p 1-1-0; patellae p 0-1-0; femora d 0-2-4. *Epigyne* (Fig. 21C, F, G): thinly covered by rather coarse blackish hairs.

Dimensions (mm): total length 5·52; carapace length 2·6, breadth 2·06, height 1·56; abdomen length 2·84; eyes, anterior row 1·96, middle row 1·9, posterior row 2·0; quadrangle length 1·4 (53 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 15 : 9 : 5·5 : 8; AL–AM–PL :: 11–9; AM : CL :: 15 : 4.

VARIATION. A paratype ♂ measures 4·72 mm total length, 2·08 mm carapace length. ♀ total length varies from 4·4 to 5·52 mm, carapace length 2·16–2·6 mm (three specimens). In the paratype male the marginal cephalic bands and thoracic stripe are more conspicuous than

in the holotype, while in females the spermathecae are sometimes less evident than those shown in (Fig. 21C).

DISTRIBUTION. Malaysia.

MATERIAL EXAMINED. **West Malaysia,** Batu, village about 8 miles north of Kuala Lumpur: holotype ♂, beaten from low growing vines by standing water, 14.ix.1973 (*A. D. Blest,* Batu 33(D)) (BMNH. 1981.12.31.9); paratype ♀, beaten from creepers in damp open forest, ix.1973 (*A. D. Blest,* Batu 12 (C)) (BMNH. 1981.12.31.10); paratype ♀, from vines in dense humid forest. 13.ix.1973, (*A. D. Blest,* Batu 28 (C)) (BMNH, 1981.12.31.11). Sarawak, Gunung Mulu National Park, R.G.S./Sarawak Government Expedition, alluvial forest environs of base camp, (*F. R. Wanless*): paratype ♀, beaten from shrubs, 6.vii.1978 (BMNH. 1981.12.31.12); paratype ♂, from litter, 21.vi.1978 (BMNH. 1981.12.31.13).

Genus *COCALUS* Koch

REMARKS. This small Oriental and Australasian genus comprised of four known species (see check list) has been revised recently (Wanless, 1981*b*). The low elevation in the centre of

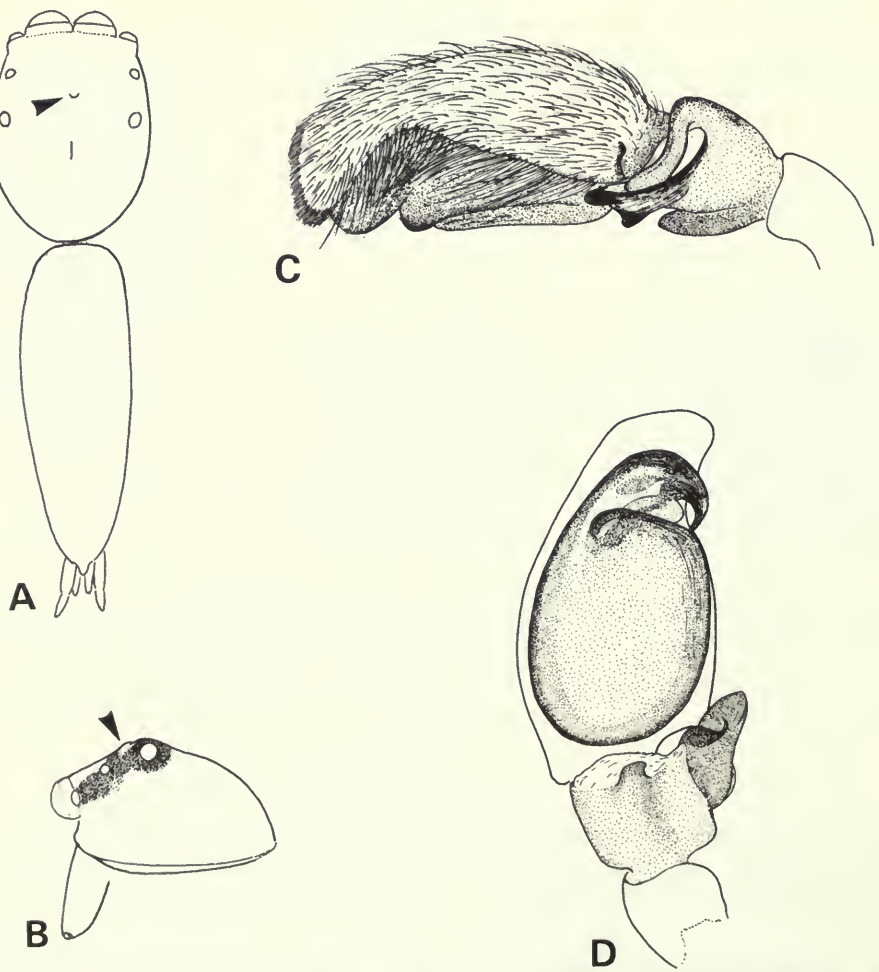

Fig. 22 *Cocalus limbatus* Thorell, holotype ♂: A, dorsal; B, carapace, lateral; C, palp, retrolateral; D, palp, ventral.

the posterior ocular quadrangle (Fig. 22A, B) and the curious finger-like projection resting on the male palpal retrolateral tibial apophysis (Fig. 22C) are diagnostic for the genus.

Its affinities are uncertain, but some possibilities are discussed elsewhere (p. 143).

Genus ***BRETTUS*** Thorell

REMARKS. This genus is comprised of six species (see check list) from India, Sri Lanka, Burma, Sulawesi and Madagascar (Wanless, 1979, 1980*a*).

The males are of considerable interest because the first pair of legs possess gutter-like femoral organs (Fig. 32A–C), and the palps, a tubular process which arises from a flask-shaped vacuole which lies near or alongside the retrolateral tibial apophysis (Figs 23D, F; 33C–E). Furthermore the tegular furrow of at least one species, *B. cingulatus* Thorell, has a minute pore (Fig. 36C, D) similar to that found in *Phaeacius lancearius* (Thorell). The function of these organs can only be guessed at (see p. 140) and they are of little use in determining the affinities of *Brettus* which are discussed elsewhere (p. 144).

The unknown male of *B. anchorum* Wanless has recently been discovered in the collections of BMNH and it is described to illustrate many of the features of the genus.

Brettus anchorum Wanless
(Fig. 23A–H)

Brettus anchorum Wanless, 1979: 188, ♀. Holotype ♀, India, Madras (BMNH) [examined].

Male from Madras, in poor condition. *Carapace* (Fig. 23A, C): amber; irregularly clothed in fine iridescent setae with broad marginal white haired bands edged above in clear brown-black hairs. *Eyes*: with black surrounds except anterior medians; fringed in pale amber hairs. *Clypeus*: white haired. *Chelicerae*: moderately robust, slightly inclined anteriorly; amber; basally a transverse fringe of white hairs with scanty covering of clear light amber ones elsewhere; promargin with three teeth, retromargin with three or four. *Maxillae and labium*: light orange-brown tinged with some grey. *Sternum* (Fig. 23G): yellow-brown with darker margins; clothed in testaceous hairs. *Coxae*: yellow-brown, first pair slightly darker. *Abdomen*: damaged, elongate ovoid; yellow-brown, lightly tinged black with paler region posteriorly. *Legs*: long and slender with black ventral fringes on tibiae and femora of the first and to a less marked degree, second pair of legs; femoral organ a minute elongate broken furrow; legs I orange-brown, others yellow-brown; spines moderately strong and numerous. Spination of legs I: metatarsi v 2-0-0, p 1-1-1, d 0-1-0, r 1-0-1; tibiae v 2-2-0, p 1-0-1, d 1-1-1; patellae p 0-1-1; femora p 1-1-0, d 0-2-3, r 1-1-0. *Palp* (Fig. 23D–F, H): M_1 and M_3 are both slender translucent prongs, whereas M_2 forms an oblique translucent ledge which appears to arise from a sclerotised base that runs parallel with the oblique portion of M_3; notice also the apophysis 'a' protruding from below the tegulum.

Dimensions (mm): total length c. 5·6; carapace length 2·48, breadth 2·10, height 1·36; abdomen length c. 3·24; eyes, anterior row 1·32, middle row 1·04, posterior row 1·14; quadrangle length 1·02 (41 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 11·5 : 6 : 4·5 ; 6; AL–PM–PL :: 6–9; AM : CL :: 11·5 : 5.

DISTRIBUTION. India.

MATERIAL EXAMINED. India: holotype, ♀, data as in synonymy; 1♂, Ootacamund, Madras, purchased from G. F. Hampson, BMNH. 1888.57.

REMARKS. The elements M_1 M_2 and M_3 are less well developed or even lacking in other species of *Brettus*; apophysis 'a' is also evidently absent.

Genus ***NEOBRETTUS*** gen. n.

DEFINITION. Small squat hairy spiders (2·0 to 4·0 mm total length). Sexual dimorphism not marked.

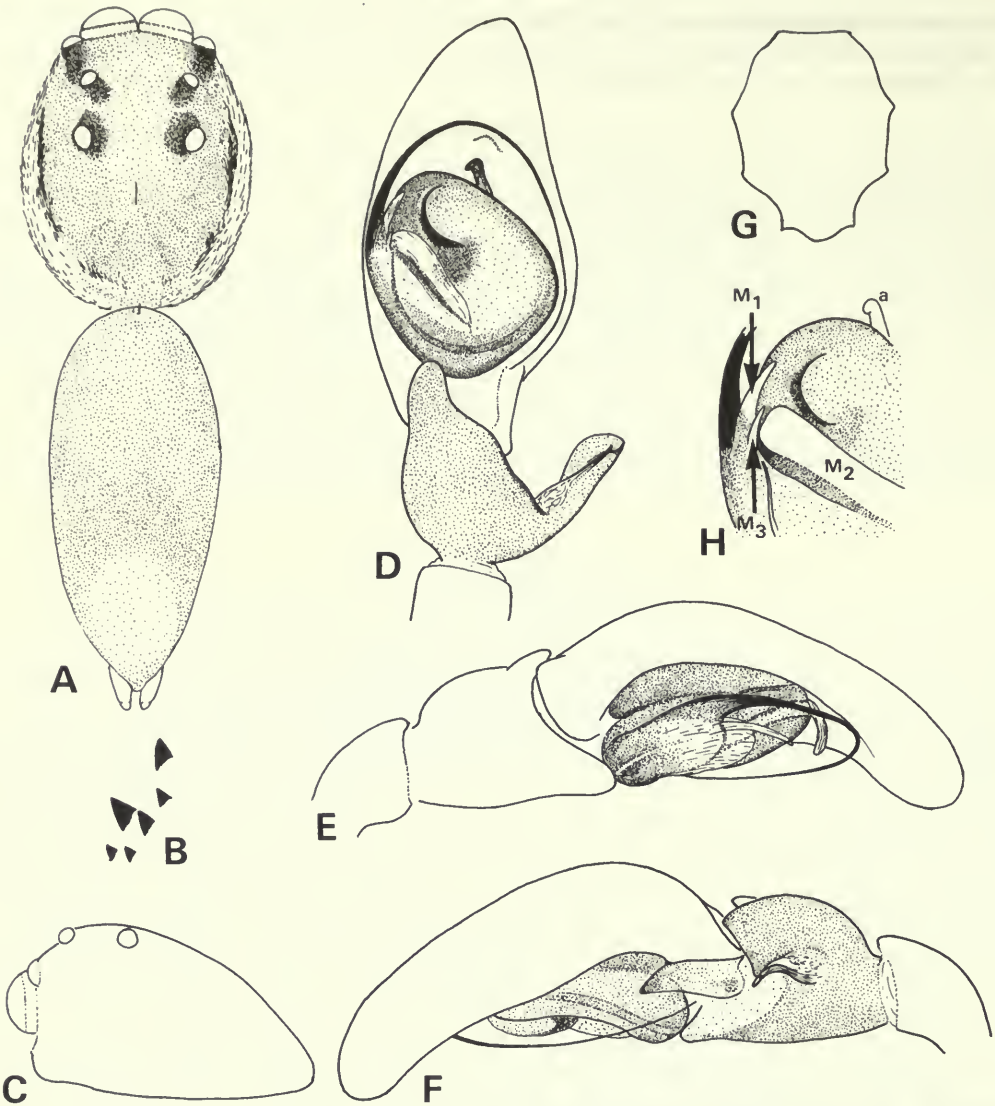

Fig. 23 *Brettus anchorum* Wanless, ♂: A, dorsal; B, cheliceral teeth, inner view; C, carapace, lateral; D, palp, ventral; E, palp, prolateral; F, palp retrolateral; G, sternum; H, distal haematodocha, tegular ledge and apophysis 'a'.

Carapace (Fig. 24A, B): moderately high, greatest height near middle of thoracic part, slightly longer than broad, widest at level of coxae III; fovea of medium length, positioned more or less midway between posterior lateral eyes; sides clothed in long hairs. *Eyes*: with moderately large lenses set on low tubercles; anteriors subcontiguous with apices recurved in frontal and dorsal views; anterior medians largest; anterior laterals about half diameter of anterior medians with noticeably dorsal direction of regard; posterior medians relatively large, positioned slightly closer to and more or less on optical axis of anterior laterals; posterior laterals slightly smaller or as large as anterior laterals and positioned inside lateral margins of carapace when viewed from above; posterior ocular quadrangle broader than long and wider behind; entire quadrangle about 56 per cent of carapace length. *Clypeus*: moderately high. *Chelicerae*: small, more or less parallel and slightly inclined anteriorly; fang

slender and curved; promargin with three teeth, retromargin with four of five. *Maxillae*: moderately long, more or less parallel with rounded outer distal margins. *Labium*: about as long as broad and about half maxillae length. *Sternum* (Fig. 24F): elongate scutiform. *Abdomen*: subovoid, slightly broader behind; spinnerets moderately long, posteriors moderately robust and slightly shorter than robust anteriors, medians slender and shorter than others; tracheal spiracle and position of colulus obscure, presumably in usual location near base of spinnerets. *Legs*: moderately long and slender with stout ventral fringes on tibiae, patellae and femora of legs I; femoral organ evidently lacking; patellae and tibiae together somewhat bowed, a characteristic emphasised by curving black lateral stripes; spines numerous and moderately strong; claws pectinate, tufts present, scopulae absent. *Female palps*: long and slender with distal claw. *Male palps*: moderately complex; interlocking tubercles well developed especially between cymbium/tibiae; patellae with slight anterodorsal tubercle; tibiae with pronounced anterodorsal tubercle, broad retrolateral apophysis bearing an inner flange, a rather elongate ventral apophysis and a minute intermediate apophysis (arrowed, Fig. 24D); cymbium with distal scopulae, basal excavations and protuberances; embolus long slender and flattened, arising from anterolateral margin of tegulum; distal haematodocha an obscure membraneous patch M_1 and an ill-defined whitish area M_2, the former bearing a large petal-like lobe (arrowed, Fig. 24D); tegulum subtrapezoid with a broad open furrow whose outer wall bears a groove forming an embolic guide, an oblique fine distal ledge M_3 and a distally sinuous peripheral seminal duct; median haematodocha, subtegulum and basal haematodocha not examined. *Epigyne*: relatively large; copulatory openings positioned laterally, introductory ducts evidently with one spiral and then opening into flask shaped spermathecae.

TYPE SPECIES: *Cyrba tibialis* Prószyński.

ETYMOLOGY. The genus name means newly related to *Brettus*; the gender is feminine.

DIAGNOSIS. As the only known species is squat and hairy it is unlikely to be confused with other taxa in the subfamily.

Neobrettus tibialis (Prószyński) comb. n.
(Fig. 24A–H)

Cyrba tibialis Prószyński, 1978: 19. Holotype ♂, Bhutan (NHM, Basel) [examined].

DIAGNOSIS. By the squat hairy body (Fig. 24A).

Male from Malaysia, in good condition. *Carapace* (Fig. 24A, B): pale yellow suffused and mottled black with whitish subcutaneous guanin in eye region and vertical pale yellowish stripes on sides above coxae I to III; clothed in long black, and whitish hairs on sides with short light brown iridescent ones dorsally. *Eyes*: with black surrounds except anterior medians; fringed by whitish, and light brown iridescent hairs. *Clypeus*: suffused black; clothed in long whitish, and pale grey-yellow hairs. *Chelicerae*: whitish yellow suffused with some black; shiny; basally clothed in short more or less recumbent pale yellow hairs, distally in scattered long pale orange ones; promargin with three teeth, retromargin with five. *Maxillae and labium*: whitish yellow. *Sternum*: whitish yellow clothed in light yellowish hairs. *Coxae*: whitish yellow. *Abdomen*: pale grey with light yellowish subcutaneous guanin; irregularly clothed in minute iridescent setae with patches of short light brown lanceolate hairs, and anteriorly a fringe of mixed stout black and fine whitish hairs; ventrally pale greyish yellow with whitish guanin. *Legs*: moderately long and slender with patellae and tibiae of legs II to IV slightly bowed (Fig. 24E, G); legs I femora whitish yellow suffused black on sides, patellae, tibiae and metatarsi whitish yellow with longitudinal black prolateral stripes and ventral fringes of stout black hairs, tarsi whitish yellow; other legs whitish yellow with black transverse stripes on inside of femora and black longitudinal stripes on inside of patellae and tibiae; spines moderately strong and numerous. Spination of legs I:

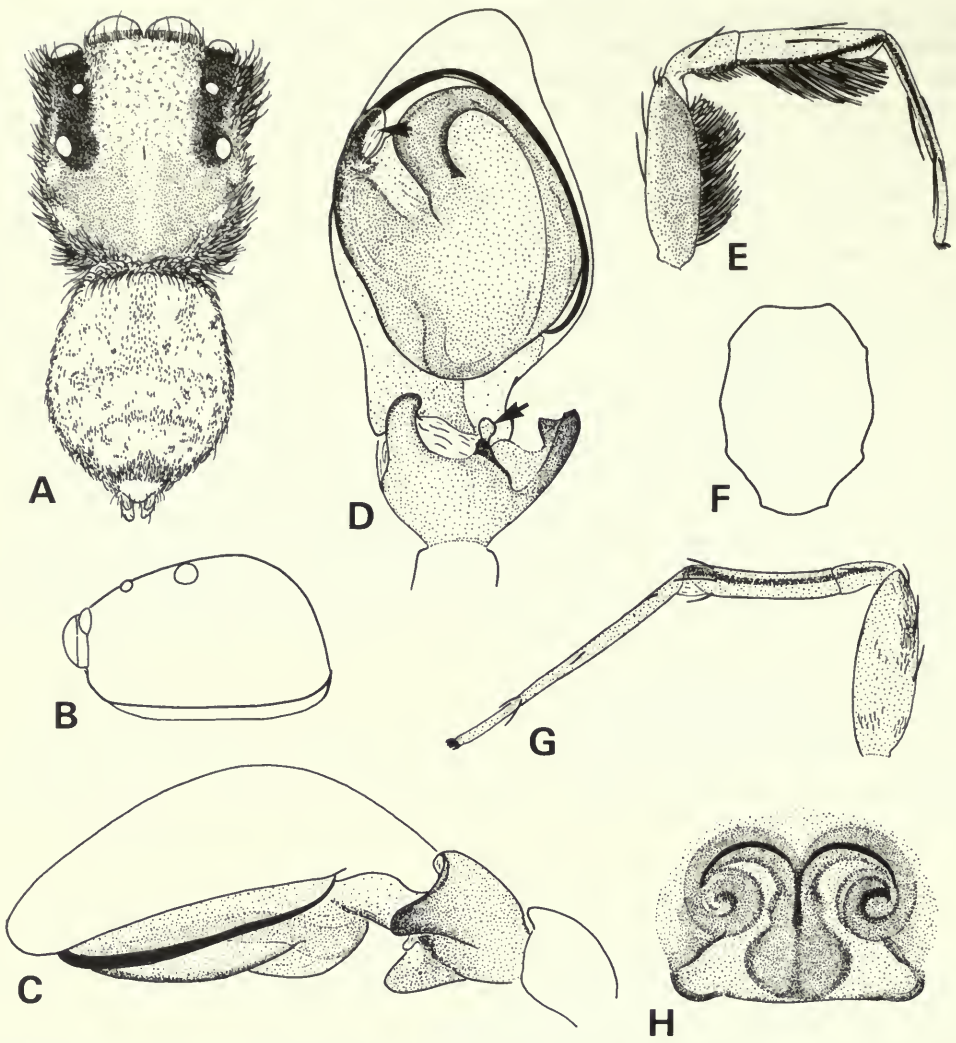

Fig. 24 *Neobrettus tibialis* (Prószyński), ♂: A, dorsal; C, palp, retrolateral; D, palp, ventral; E, leg I; G, leg IV. ♀: B, carapace, lateral; F, sternum; H, epigyne.

metatarsi v 0-2-1, p 0-1-1, d 0-1-2, r 0-1-1; tibiae v 1-2-2, p 0-1-1, d 0-1-0, r 0-1-1; patellae p 0-1-0, r 0-1-0; femora d 0-2-4. *Palp* (Fig. 24C, D).

Dimensions (mm): total length 3·2; carapace length 1·7, breadth c. 1·48, height 1·04; abdomen length 1·64; eyes, anterior row 1·33, middle row 1·07, posterior row 1·29; quadrangle length 0·96 (56 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 10 : 5·5 : 3 : 5; AL–PM–PL :: 6·5–7; AM : CL :: 10 : 4.

Female, formerly undescribed, from Malaysia in good condition. *Carapace*: similar to ♂, but markings slightly more distinct. *Eyes*: fringed by whitish hairs. *Clypeus*: sparsely white haired with scattered black ones. *Chelicerae*: pale yellow-brown with sooty markings; thinly covered in fine light brownish hairs; promargin with three teeth, retromargin with four or five. *Maxillae and labium*: pale yellow-brown lightly suffused with some black. *Sternum* (Fig. 24F): whitish yellow with darker margins; thinly clothed in pale yellowish hairs. *Coxae*: whitish yellow. *Abdomen*: similar to ♂, but whitish guanin forming more distinct transverse bands. *Legs*: first pair with femora whitish yellow heavily tinged black on sides with scanty

dorsal fringe of black hairs and ventral fringe, comprised of stout black hairs inside and fine whitish ones on outer, other segments whitish yellow with curving black stripe on outer side of patellae, tibiae and metatarsi, also on patellae and tibiae a ventral fringe of fine greyish, and white hairs, the former restricted to patellae and basal region of tibiae; other legs lacking fringes; legs II–III pale yellow with black blotches on femora and curving black lateral stripes on inner sides of patellae and tibiae II and on outer sides of patellae and tibiae III; legs IV similar to III, but with black lateral stripes on sides of tibiae only. Spination of legs I: metatarsi v 0-2-1, p 0-1-1, d 0-1-2, r 0-2-0; tibiae v 0-2-1, p 1-0-1, d 0-1-0; patellae p 0-1-0, r 0-1-0; femora d 0-2-4. *Epigyne* (Fig. 24H).

Dimensions (mm): total length 4·0; carapace length 1·76, breadth 1·58, height 1·2; abdomen length 2·4; eyes, anterior row 1·32, middle row 1·14, posterior row 1·4; quadrangle length 1·0 (56 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 10 : 5·2 : 3 : 5·2; AL–PM–PL :: 7–7·5; AM : CL :: 10 : 5.

VARIATION. ♂ total length varies from 2·76 to 3·2 mm, carapace length 1·48–1·7 mm (four specimens). Another ♀ measures 3·28 mm total length, and c. 1·6 mm carapace length.

Some of these specimens are darker than those described above and in the female the epigyne is less distinct, but nevertheless still comparable with Fig. 24H.

DISTRIBUTION. India: Bhutan; Malaysia.

MATERIAL EXAMINED. **Bhutan**: Phuntsholing, holotype ♂, 21.iv.1972 (Basal Natural History Museum Expedition to Bhutan, 1972). **Malaysia**: Genting, about 30 miles NE Kuala Lumpur, under dead banana trees, 1♂, 1♀, 18–22.viii.1979 (*J. & F. Murphy* coll.) (BMNH. 1982.2.4.1–2), 1♀, 2♂♂, (*J. & F. Murphy* coll.); Johore, Layang-Layang, 21–23. vii.1979, 1♀, (*J. & F. Murphy* coll.).

Genus ***CYRBA*** Simon

According to Roewer (1954) *Cyrba* is comprised of 11 species, of these at least two, *C. dotata* Peckham & Peckham and *C. armillata* Peckham & Peckham, have been misplaced and are not included in the check list (p. 194). Three other species are also excluded, *C. tibialis* Prószyński is made the type species of a new genus (see above), while *C. flavimanus* Simon and *C. tadzika* Andreeva are junior synonyms of *C. micans* Simon (Prószyński, 1978). A revision of the genus is in preparation, but studies are at an early stage and remarks are based mainly on the type species, *C. algerina* (Lucas), figures of which are provided for comparative purposes.

Cyrba unlike many salticid genera is fairly easy to recognise by the combined presence of small posterior median eyes, elongate fovea and numerous cheliceral teeth. Some species have abdominal patterns and are brightly coloured, but in other respects their general habitus is rather similar, the genitalia providing as usual the more important diagnostic features. Although *Cyrba* cannot at present be supported by uniquely derived characters the genus nevertheless appears to be valid and would seem to belong in the *Brettus/Neobrettus* complex, while at the same time showing similarities with *Portia*. The epigynes of some species of *Cyrba* and *Portia* are structurally alike, especially in *C. algerina* and *P. fimbriata*. Also, in males of both genera the palpal organs possess a dorsal projection, small in *Cyrba*, large in *Portia*, on the basal margin of the cymbium (Fig. 25B, arrowed). Other palpal similarities are also evident, as noted by Prószyński (1978), but in contrast the development of the retrolateral tibial apophyses seems to be quite different from those of *Portia*. However, it is possible that too much importance is being attached to this character as the paired tibial apophyses of *C. algerina* (Fig. 25B, F) are possibly unique, since other mostly unidentified species of *Cyrba* possess only a single apophysis bearing hyaline elements similar to those found in *Taraxella*.

The inclusion of *Cyrba* in the Plexippinae (Prószyński, 1976) is unjustified, as is also its original placement in the Thiodininae (Petrunkevitch, 1928) since it lacks the characters of either subfamily.

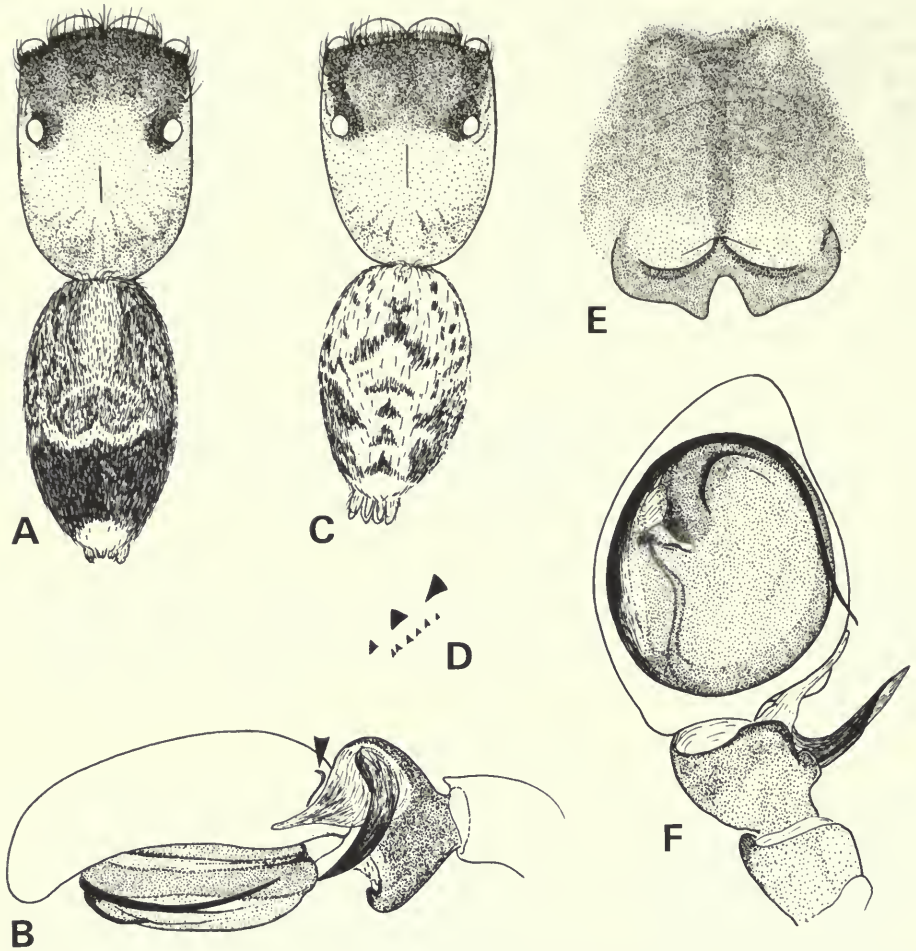

Fig. 25 *Cyrba algerina* (Lucas), ♂: A, dorsal; B, palp, retrolateral; F, palp, ventral. ♀: C, dorsal; D, cheliceral teeth, inner view; E, epigyne.

Genus ***MELEON*** gen. n.

Portia Karsch, 1878: 774 [in part].

DEFINITION. Spiders of medium size (i.e. between 4·0 and 8·0 mm in length). Patterns not distinctive, preserved specimens usually orange-brown to pale yellowish brown with vague sooty abdominal chevrons and sometimes light flecking; often clothed in minute whitish/iridescent setae; posterior median eyes sometimes with pronounced hair tuft posteriorly; legs I, at least in African species with strong ventral fringes.

Carapace: high, usually with an abrupt slope from about level of posterior median eyes to anterior eye row; longer than broad, widest at about level between coxae II and III; fovea moderately long and sulciform, positioned a little behind posterior margins of posterior lateral eyes. *Eyes*: with moderately strong lenses set on moderately low tubercles; anteriors subcontiguous or closely spaced with apices weakly to strongly recurved in frontal view; anterior medians largest; anterior laterals slightly larger than half diameter of anterior medians; posterior medians large, positioned slightly nearer to and on or slightly inside optical axis of anterior laterals; posterior lateral eyes slightly smaller or as large as anterior laterals and situated inside lateral margins of carapace when viewed from above; posterior

ocular quadrangle broader than long and wider behind; entire quadrangle between 38 and 50 per cent of carapace length. *Clypeus*: moderately high, concave. *Chelicerae*: moderately robust, more or less parallel and slightly inclined anteriorly; fang moderately robust and curved; promargin with three teeth, retromargin with three to six. *Maxillae*: moderately long, parallel or slightly diverging with rounded outer distal margins. *Labium*: about as long as wide and about half maxillae length. *Sternum*: generally scutiform. *Abdomen*: generally elongate ovoid; spinnerets moderately long, posteriors moderately robust and slightly longer than robust anteriors, medians slender and shorter than others. *Legs*: long and slender with numerous moderately strong spines, femoral organ lacking; legs I sometimes with strong fan-like fringes on venter and dorsum of tibiae, venter of femora and to a less marked degree on venter of patellae; also, on legs II and IV sometimes a ventral fringe more or less limited to tibial apices; claws pectinate; tufts present, scopulae absent, but minute setae present (c.f. *Portia*). *Female palps*: moderately long, rather slender with apical claw. *Male palps*: complex, interspecifically fairly distinct with dorsal interlocking tubercles variable between cymbium/tibiae and weak between tibiae/patellae; tibiae with ?moveable dorsal or retrolateral apophysis arising from a membraneous joint, and ventral apophyses which vary in development; cymbium distally scopulate, sometimes modified apically to accommodate embolic region, basally excavated or scalloped with raised sclerotised margins sometimes surrounding an indistinct subtriangular membraneous area similar to, but evidently not contiguous with connective tissue of the cymbial/tibial joint; embolus arising apically, short and slender to moderately long and robust curving inwards towards alveolus or outer edge of cymbium; distal haematodocha an obscure membraneous patch M_1 which sometimes bears a minute lobe, region M_2 sometimes patch-like but generally not evident being largely obscured by tegular element M_3; tegulum subovoid, with deep peripheral furrow and distal lobe-like region bearing the embolus, distal haematodocha, and distal element M_3 which often has a small delicate lobe that extends laterally as a fine delicate ledge which terminates in the furrow and appears to function as an embolic guide; median haematodocha, subtegulum and basal haematodocha not examined. *Epigynes*: relatively large and interspecifically distinct; internal structures poorly known—only examined in one species (*M. solitaria* (Lessert)). In this, obscure anteriorly situated copulatory openings are separated by an indistinct median groove, apparently lacking in other species; the introductory ducts are moderately long, gently curving and open distally into large dark spermathecae bearing short slender fertilisation ducts near posterior margin.

TYPE SPECIES. *Portia kenti* Lessert.

ETYMOLOGY. The genus name is an abritrary combination of letters; the gender is considered feminine.

DIAGNOSIS. Species of this genus superficially resemble those of *Portia, Brettus* and *Veissella,* but they are not likely to be confused for in practice the epigynes are quite distinct (see Wanless, 1978*b*) and the male palps easily recognised by the membraneous socket of the tibial apophyses (Figs 26F: 34C–E).

Meleon solitaria (Lessert) comb. n.
(Fig. 26A–G)

Portia solitaria: Wanless, 1978: 91 [synonymy and ♀ description].

Male, formerly undescribed, in poor condition. *Carapace* (Fig. 26A, C): orange-brown with blackish margins and mottling on lower thoracic sides; weakly iridescent under some angles of illumination; irregularly clothed in short fine whitish hairs with pale amber tufts behind posterior median eyes. *Eyes*: with black surrounds except anterior medians; anterior row strongly recurved in frontal view; fringed by dull amber hairs with paler tips. *Clypeus*: thinly covered in short whitish hairs mixed with long brownish ones. *Chelicerae*: moderately robust; orange-brown mottled black; iridescent; thinly clothed in short clear whitish hairs and long

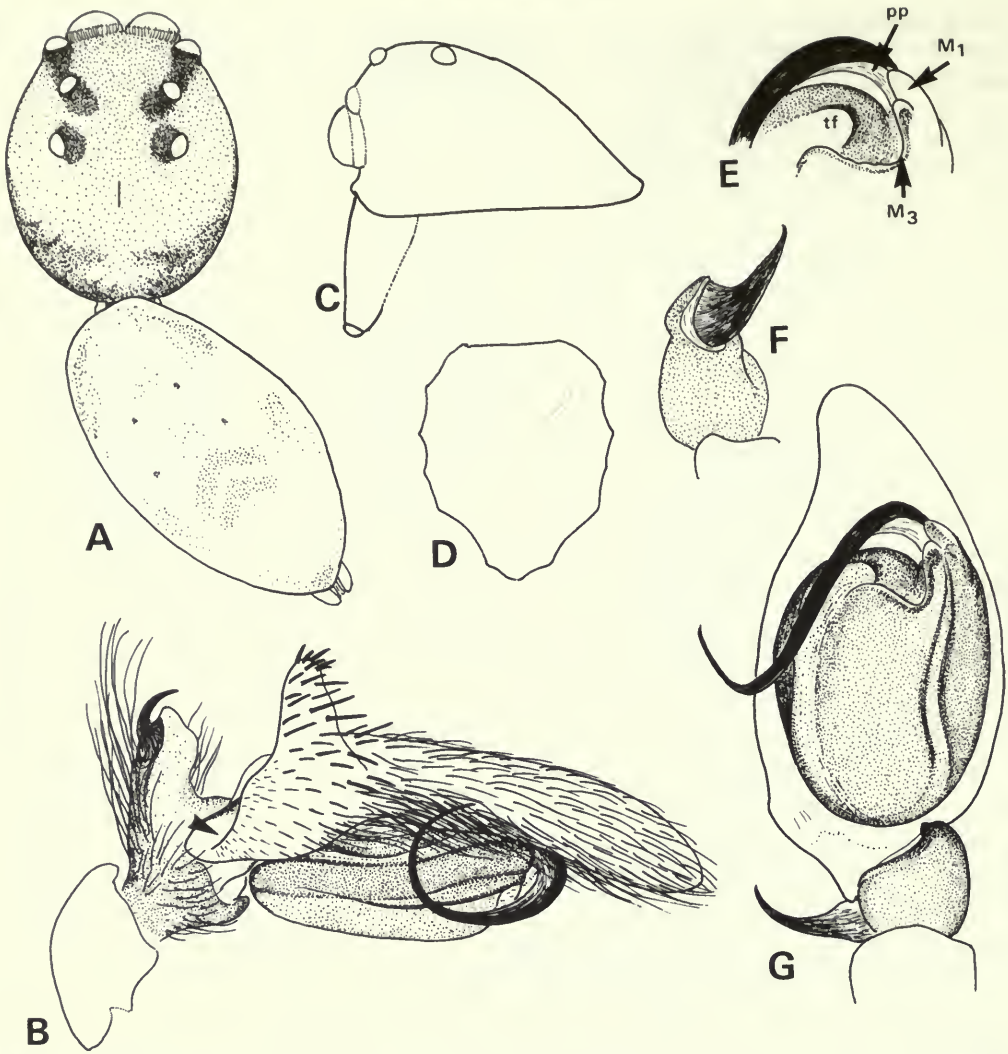

Fig. 26 *Meleon solitaria* (Lessert), ♂: A, dorsal; B, palp, retrolateral; C, carapace, lateral; D, sternum; E, distal haematodocha and tegular ledge; F, retrolateral tibial apophysis, dorsal; G, palp, ventral. Abbreviations: pp, pars pendula; tf, tegular furrow.

pale brownish ones; promargin with three teeth, retromargin with four. *Maxillae and labium*: yellow-brown tinged black. *Sternum* (Fig. 26D): orange-brown tinged black, shiny, thinly clothed in clear whitish hairs with brownish ones more or less opposite coxae. *Coxae*: first pair orange-brown lightly tinged black, rest paler. *Abdomen*: dull yellow-brown tinged grey with vague dorsal chevrons and broad longitudinal black stripe ventrally; irregularly clothed in fine pale amber/iridescent setae. *Legs*: long and slender; legs I generally dark orange-brown, but apices of patellae and femora paler, with strong black ventral and dorsal fringes on tibiae and ventral ones on femora—mostly rubbed; other legs orange-brown with blackish markings on metatarsi and femora IV, also short fringes and blackish annuli on apices of tibiae IV; spines moderately strong and numerous. Spination of legs I: metatarsi v 2-0-2, p 1-0-1, d 0-1-0, r 1-1-1; tibiae v 2-1-0, p 1-0-1, d 1-1-0, r 1-0-1; patellae p 0-1-0, r 0-1-0; femora p 1-1-1, d 1-1-3, r 1-1-1. *Palp* (Fig. 26B, E–G): typical of genus except for spinose protuberance on cymbium.

Dimensions (mm): total length c. 5·6; carapace length 2·36, breadth 2·22, height 1·68; abdomen length 3·2; eyes, anterior row 1·48, middle row 1·12, posterior row 1·32; quadrangle length 1·2 (50 per cent of carapace length). *Ratios*: AM : AL : PM : PL :: 13·4 : 7·5 : 6 : 7; AL–PM–PL :: 7·5–9·4; AM : CL :: 13·4 : 6·5.

DISTRIBUTION. Guinea; Ivory Coast; Zaire.

MATERIAL EXAMINED. **Ivory Coast**: environs of Kotiessou, nr. Bandama River, 1♂, from *Piliostigma thonningei* (Schum) Milne Redhead, a small tree common in savannah, (*J. Jezequel,* PNB. 145) (MNHN, Paris).

Genus *VEISSELLA* gen. n.

Portia (Karsch, 1878: 774 [in part].

DEFINITION. Spiders of medium size (i.e. between 4·0 and 8·0 mm in length). Sexual dimorphism not marked, patterns of preserved specimens not very distinctive—generally orange-brown with whitish yellow abdomen bearing a ventral black stripe, clothed in fine whitish/iridescent setae; legs I and II with strong ventral fringes.

Carapace: high with an abrupt slope from about level of posterior median eyes to anterior eye row; longer than broad, widest at level between coxae II and III; fovea moderately long and sulciform, apex at level of posterior margins of posterior lateral eyes. *Eyes*: with moderately strong lenses set on moderately low tubercles; anteriors subequally spaced and closely set with apices strongly recurved in frontal view; anterior medians largest; anterior laterals slightly larger than half diameter of anterior medians; posterior medians large and positioned slightly nearer to and more or less on optical axis of anterior laterals; posterior lateral eyes slightly smaller than anterior laterals and situated inside lateral margins of carapace when viewed from above; posterior ocular quadrangle broader than long and wider behind; entire quadrangle between 42–45 per cent of carapace length. *Clypeus*: moderately high, concave. *Chelicerae*: moderately robust, more or less parallel; vertical or slightly inclined anteriorly; fang moderately robust or curved; promargin with three teeth, retromargin with three or four. *Maxillae*: moderately long, more or less parallel with rounded outer distal margins. *Labium*: about as long as broad and about half maxillae length. *Sternum*: elongate scutiform. *Abdomen*: elongate ovoid, spinnerets moderately long, posteriors moderately robust and about as long as robust anteriors, medians slender and slightly shorter than others. *Legs*: long and slender with numerous strong spines; femoral organs lacking; legs I and to a lesser extent II, with strong ventral fringes; claws pectinate, tufts present, scopulae absent, but with minute iridescent setae, (c.f. *Portia*). *Female palps*: moderately long and slender with apical claw. *Male palps*: complex, intergenerically distinct; lacking dorsal interlocking tubercles on cymbium/tibial joint, but with pronounced anterodorsal tubercle on patellae; also on patellae a large retrobasal apophysis opposing a similar but larger femoral apophysis bearing on its inner surface curving recumbent setae; tibiae with an oblique ventral apophysis and broad flange-like retrolateral apophysis; cymbium with distal scopulae, lacking excavations or protuberances; embolus arising apically, moderately long and slender, but sinuous and curving inwards towards alveolus; distal haematodocha with membraneous patch M_1 bearing a minute delicate lobe, M_2 an indistinct region giving rise to a large sclerotised lobe (Fig. 27G, arrowed). Tegulum subovoid with an open furrow extending a short distance around prolateral margin, a distal tegular ledge M_3 and lobe-like region bearing the distal haematodocha and embolus; median haematodocha, subtegulum and distal haematodocha not examined. *Epigyne*: with anterior copulatory openings divided by median guide; introductory ducts short and curving; spermathecae large, dark and contiguous with fertilisation ducts on posterior margin.

TYPE SPECIES. *Portia durbanii* Peckham & Peckham.

ETYMOLOGY. The genus name is an arbitrary combination of letters; the gender is considered feminine.

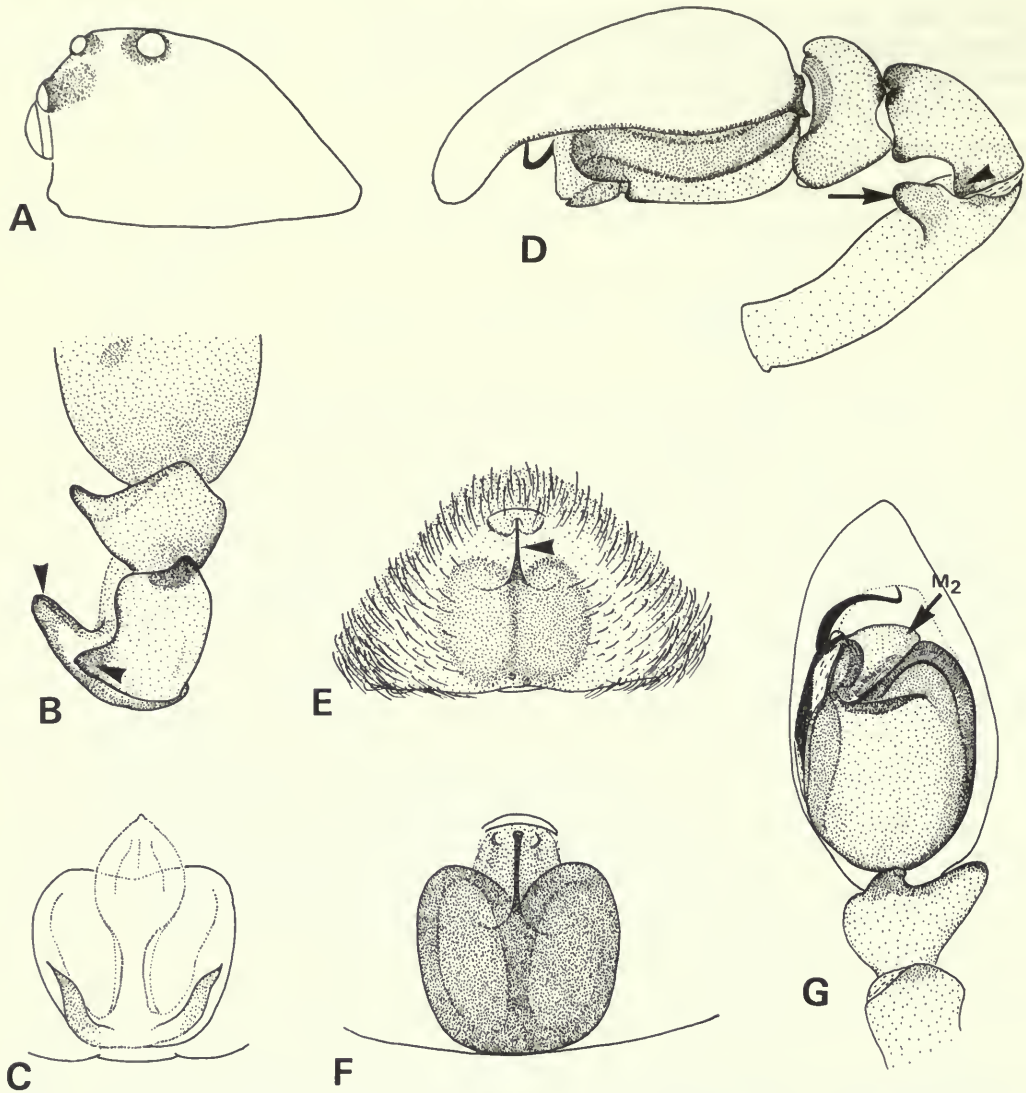

Fig. 27 *Veissella durbanii* (Peckham & Peckham), ♂: A, carapace, lateral; B, palpal tibia, patella and femora, from above; D, palp, retrolateral; G, palp, ventral. ♀: vulva, inner view; E, epigyne; F, vulva, outer view.

DIAGNOSIS. The only known species in this genus resembles those of *Meleon, Brettus* and *Portia,* but it is easily distinguished by the opposing apophyses on the male palpal patellae and tibiae (Fig. 27B, D), and median epigynal guide in females (arrowed, Fig. 27E).

Genus ***PHAEACIUS*** Simon

Phaeacius: Wanless, 1981: 199 [synonymy, definition and species descriptions].

REMARKS. A small Oriental genus comprised of five species (see check list). Most are relatively large in size (total length between 7·5 and 11·5 mm) and somewhat flattened in profile. Males are easily recognised by the massive retrolateral tibial apophyses and filamentous process M_1 (e.g. Fig. 28A, C). Females are more difficult, the best diagnostic feature being

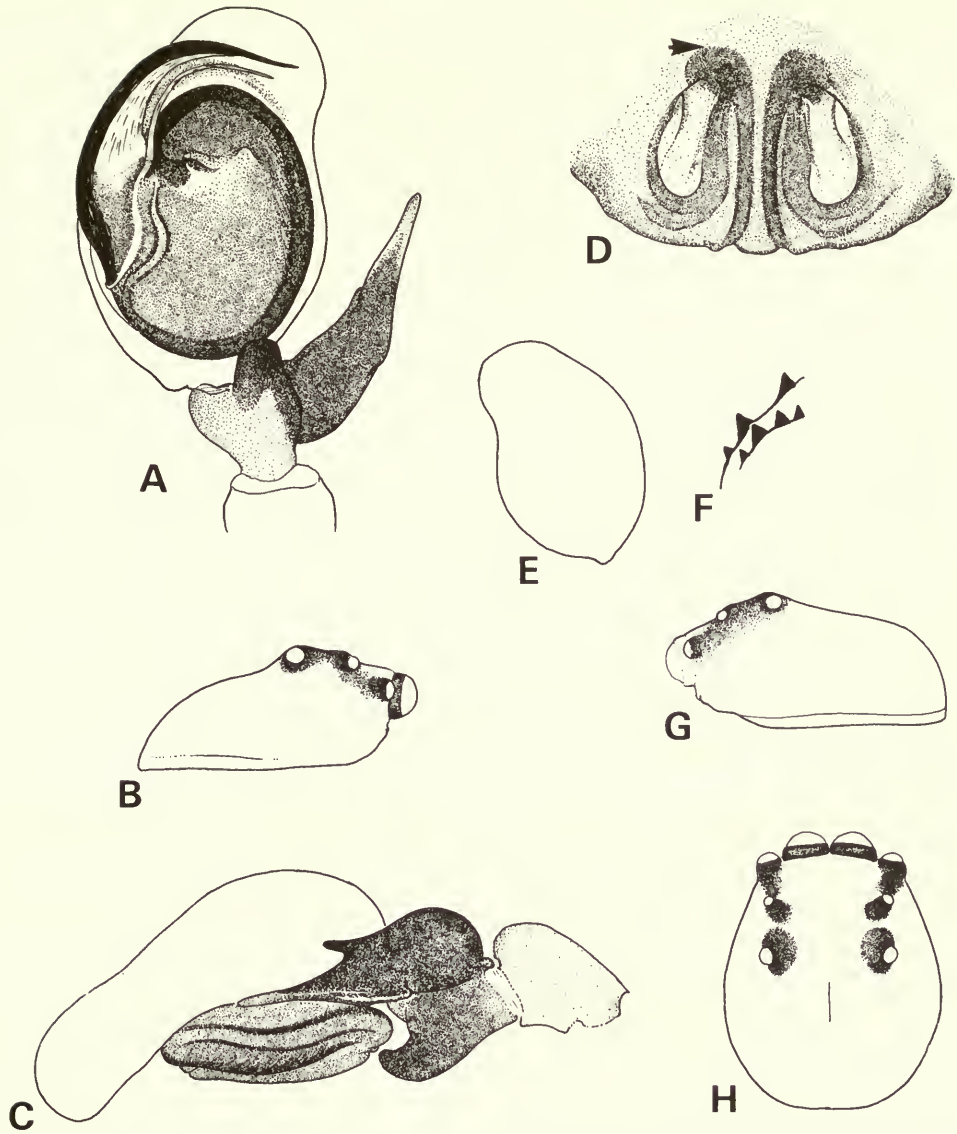

Fig. 28 *Phaeacius fimbriatus* Simon, ♂: A, palp, ventral; C, palp, retrolateral; E, cymbium, dorsal; G, carapace, lateral. ♀: B, carapace, lateral; D, epigyne; F, cheliceral teeth, inner view; H, carapace, dorsal.

the patch of fine spatulate setae on the underside of coxae IV. Its affinities are uncertain (see p. 144), but *Portia* is possibly its closest relative.

Two new records have been noted since the genus was revised (Wanless, 1981). *P. malayensis* Wanless: 1♀, collected from a *web* together with a juvenile specimen of *Portia,* Pasir Kis, Singapore, (Joseph Koh) 1982; another specimen, 1♂, (1901, BMNH. coll.) was taken from tree trunks and described by the collector as 'very protectively coloured'.

Genus ***PORTIA*** Karsch

Portia: Wanless 1978: 84 [synonymy, definition and species descriptions].

The genus was redefined by Wanless (1978*b*), but some modifications are now necessary in view of proposed taxonomic changes.

DEFINITION. Cryptic spiders with ornate hair tufts and fan-like leg fringes; medium to large in size (i.e. total length between 4·0 and 16·0 mm); sexes alike in body form, but colour patterns sometimes dimorphic—males possess whitish marginal and median carapace bands which are usually less conspicuous in females.

Carapace: high with marked slope from posterior lateral eyes to anterior eye row; fovea long, apex just behind posterior margins of posterior lateral eyes. *Eyes*: anterior row weakly to strongly procurved in frontal view; posterior medians relatively large; lenses moderately strong. *Clypeus*: high, concave. *Chelicerae*: medium to large, more or less vertical, promargin with three teeth, retromargin with six. *Abdomen*: elongate ovoid with hair tufts. *Legs*: long and slender, especially tarsi and metatarsi, with strong fan-like fringes, tufts and numerous spines. *Male palps*: large and hirsute, moderately complex and intergenerically fairly distinct; cymbium with distal scopulae and basally a somewhat angular dorsal flange and a variously pronounced retrolateral one; embolus usually arising from distal prolateral margin of tegulum, and characteristically projecting laterally, moderately long slender and curved, sometimes with basal sheath; distal haematodocha with M_1 an obscure membraneous patch partly covering embolic base and M_2 a lobe-like membrane between embolic base and tegular furrow; tegulum more or less ovoid with an open furrow, peripheral seminal ducts and distal ledge M_3 which bears a small transparent lobe above and between (M_1, M_2) and sometimes a short delicate spike in the region of the furrow. *Epigynes*: relatively large, intraspecifically sometimes rather variable, openings often plugged; African species characterized by median plate forming an apparent arch between posterior margin and copulatory openings; Oriental species possess a variously developed anterior hood and caudal ledge, the latter bearing embolic guides that extend anteriorly and merge with the copulatory openings; introductory ducts of both African and Oriental species contiguous and looping distally to open into large, dark, rounded spermathecae bearing indistinct fertilization ducts on posterior margin.

DIAGNOSIS. From other genera in the subfamily by details of the genitalia (males possess a readily observable dorsal flange arrowed, Fig. 29B, F, on the palpal cymbium) and ornamentation.

REMARKS. Several important papers on the morphology and behaviour of *Portia* have appeared since the genus was revised (Wanless, 1978*b*).

Williams and McIntyre (1980) have shown that the anterior median eyes have a telephoto element which increases image size and assists the spider in stalking prey. Later studies (Blest *et al.*, 1981) indicate that the eyes of most salticids may share this design, but it is especially pronounced in *Portia*.

During the present study the development of the lenses was found to vary independently of the size of the carapace. For example, the lenses of *Phaeacius* and *Cocalus* are not pronounced and relatively small when compared with those of other genera, suggesting that their light gathering power is lower and possibly a reflection of ambient light levels of their habitats. The direction of regard of the eyes also varies, a feature first drawn to my attention by L. Forster (pers. comm.). In most species of this subfamily the eyes of the anterior row have a horizontal or slightly ventral direction of regard, sometimes the direction is the same for both anterior medians and anterior laterals, but it is not always so. In one genus, *Neobrettus*, the direction of regard is slightly dorsal and particularly evident when the facies are viewed from in front. Lens size in relation to the carapace has been noted in the generic descriptions, but it has not been practicable to indicate direction of regard which can, however, be more conveniently shown in the figures.

Jackson and Blest (1982) have provided an excellent account of the utilisation of webs and predatory versatility of *P. fimbriata* based on observations in a Queensland rainforest and the laboratory. They have shown that *fimbriata* builds two types of webs. Type I used as a resting site and type II as a more substantial structure in which the spider captures prey, moults, mates, oviposits and broods eggs. The predatory strategy includes the use of distinct tactics for capturing varied types of prey. They will enter the webs of various species and prey on the occupant by specialised leg and palp movements which vibrate the silk and at-

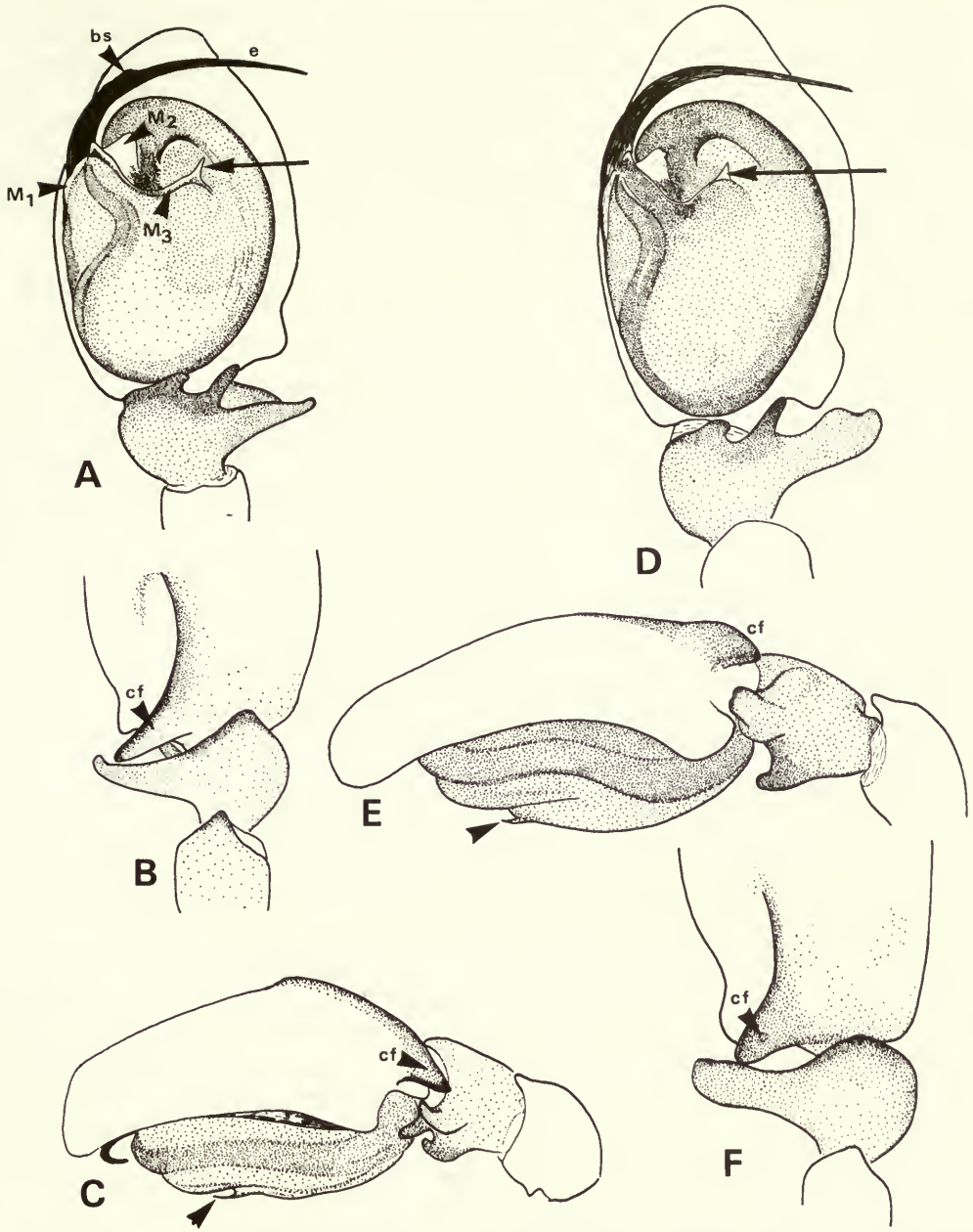

Fig. 29 (A–C) *Portia labiata* (Thorell), ♂: A, palp, ventral; B, palpal tibia and cymbial flange from above; C, palp, retrolateral. (D–F) *Portia assamensis* Wanless, ♂: D, palp, ventral; E, palp, retrolateral; F, palpal tibia and cymbial flange from above. Abbreviations: bs, basal sheath; cf, cymbial flange; e, embolus.

tract the owner to within striking distance. They also prey on other salticids outside of webs by moving in a slow mechanical fashion and stopping whenever noticed by the victim which evidently fails to recognise them as another salticid and potential predator. *Portia* also pursued insects, outside of webs, on its own web or in the webs of other spiders, but showed a preference for, and was more successful in capturing spiders. Jackson (1982) provides

additional data on intraspecific interactions and reproductive biology which will form the basis for comparative studies on other species.

Jackson and Blest (1982) proposed a hypothetical model for the evolution of both *Portia fimbriata* and typical cursorial salticids from non-visual web-building ancestors. They suggested that acute vision evolved in the context of web predation and once acquired permitted the vagrant predation of motile insects. The biology of other genera in this and related groups will undoubtedly test the model (parts of which have been collaborated by recent work, Jackson, in prep.) and provide further insight into the evolutionary events which lead to the adaptive radiation of the Salticidae.

Taxonomic summary

1. *Boethus* Thorell, 1878 is a junior homonym of *Boëthus* Foerster, 1868.
2. Spartaeinae nom. n., is proposed.
3. Six new genera are proposed:
   Meleon gen. n., *Mintonia* gen. n., *Neobrettus* gen. n., *Veissella* gen. n., and *Yaginumanis* gen. n.
4. Ten new species are described:
   Gelotia robusta sp. n., *Gelotia syringopalpis* sp. n., *Mintonia breviramus* sp. n., *Mintonia mackiei* sp. n., *Mintonia melinauensis* sp. n., *Mintonia nubilis* sp. n., *Mintoria tauricornis* sp. n., *Spartaeus thailandica* sp. n. and *Taraxella solitarius* sp. n.
5. Three species are newly synonymised:
   Boethus striatipes (Simon, 1901) and *Boethus caligatus* (Simon, 1901) are junior synonyms of *Spartaeus spinimanus* Thorell, 1878.
   Codeta bouchardi Simon, 1903 is a junior synonym of *Gelotia bimaculata* Thorell, 1892.
6. Seven new combinations are proposed:
   Gelotia argenteolimbata (Simon) comb. n., *Mintonia ramipalpis* (Thorell) comb. n., *Neobrettus tibialis* (Prószyński) comb. n., *Gelotia salax* (Thorell) comb. n., *Meleon solitaria* (Lessert) comb. n., *Veissella durbanii* (Peckham & Peckham) comb. n., and *Yaginumanis sexdentatus* (Yaginuma) comb. n.
7. The males of *Brettus anchorum* Wanless and *Meleon solitaria* (Lessert) are newly described.

Check list, known sex and distribution of species in the subfamily Spartaeinae

(*= type species)

Brettus Thorell		
B. adonis Simon	♂♀	Sri Lanka
B. albolimbatus Simon	♀	India
B. anchorum Wanless	♂♀	India
**B. cingulatus* Thorell	♂	Burma
B. celebensis (Merian)	♀	Sulawesi
B. madagascarensis (Peckham & Peckham)	♀	Madagascar
Cocalus Koch		
**C. concolor* Koch	♂	Bintang Island
C. gibbosus Wanless	♂	Australia
C. limbatus Thorell	♂	Amboina
C. murinus Simon	♀	Sumatra
Cyrba Simon		
**C. algerina* (Lucas)	♂♀	Canary Isl., Burma, India, Mediterranean Region, Nepal, Port. Guinea, Sumatra, Turkestan, W. Africa

C. bidentata Strand	♀	Ethiopia
C. bimaculata Simon	♀	Republic of Congo
C. boveyi Lessert	♂	Angola
C. nigrimana Simon	♂♀	East Africa, South Africa
C. micans Simon	♂♀	Bhutan, India, Sumatra, USSR (Tadzhikistan)
C. picturata Karsch	♀	Hong Kong
C. szechenyii Karsch	♀	Hong Kong
Gelotia Thorell		
G. argenteolimbata (Simon)	♂	Singapore
G. bimaculata Thorell	♂♀	Borneo, Sumatra
**G. frenata* Thorell	♀	Sumatra
G. robusta sp. n.	♂	New Britain
G. salax (Thorell)	♂	Sulawesi
G. syringopalpis sp. n.	♂♀	Sarawak
Meleon gen. n.		
M. falcifera (Wanless)	♂	Uganda
**M. kenti* (Lessert)	♂♀	Angola, Malawi, South Africa
M. madagascarensis (Wanless)	♂	Madagascar
M. oreophila (Wanless)	♀	Madagascar
M. russata (Simon)	♀	Madagascar
M. solitaria (Lessert)	♂♀	Guinea, Ivory Coast, Zaire
Mintonia gen. n.		
M. breviramus sp. n.	♂♀	Sarawak
M. mackiei sp. n.	♂	Kalimantan
M. melinauensis sp. n.	♂	Sarawak
M. nubilis sp. n.	♀	Kalimantan
M. protuberans sp. n.	♂	Singapore
M. ramipalpis (Thorell)	♂♀	Java, Sarawak, Sumatra
**M. tauricornis* sp. n.	♂♀	Sarawak
Neobrettus gen. n.		
**N. tibialis* (Prószyński)	♂♀	Bhutan, Malaya
Phaeacius Simon		
P. canalis Wanless	♂♀	Philippines
**P. fimbriatus* Simon	♂♀	Java
P. lancearius (Thorell)	♂	Burma, India
P. malayensis Wanless	♂♀	Singapore, Sumatra
P. saxicola Wanless	♀	Nepal
Portia Karsch		
P. africana (Simon)	♂♀	Angola, Cameroun, Central African Republic, French, Guinea, Gabon, Ghana, Ivory Coast, Sierra Leone, Zaire, Zambia
P. albimana (Simon)	♂♀	India, Sri Lanka
P. assamensis Wanless	♂♀	Assam, Malaya, Nepal
P. crassipalpis (Peckham & Peckham)	♂	Borneo, Singapore
P. fimbriata (Doleschall)	♂♀	Amboina, Australia, Mussau Isl., New Georgia, New Guinea, Solomon Isl., Sri Lanka, Yule Isl.
P. labiata (Thorell)	♂♀	Burma, India, Malaya, Sarawak, Siam, Sri Lanka, Sumatra, Philippines
P. orientalis Murphy & Murphy	♂	Hong Kong
**P. schultzii* Karsch	♂♀	French Guinea, Kenya, Madagascar, Malawi, South Africa, Tanzania, Zaire

Spartaeus Thorell		
**S. spinimanus* (Thorell)	♂♀	Amboina, Java, Sarawak, Singapore, Sri Lanka, Sumatra
S. thailandica sp. n.	♀	Thailand
Taraxella gen. n.		
**T. solitaria* sp. n.	♂	Sarawak
Veissella gen. n.		
**V. durbanii* (Peckham & Peckham)	♂♀	South Africa
Yaginumanis gen. n.		
**Y. sexdentatus* (Yaginuma)	♂♀	Japan

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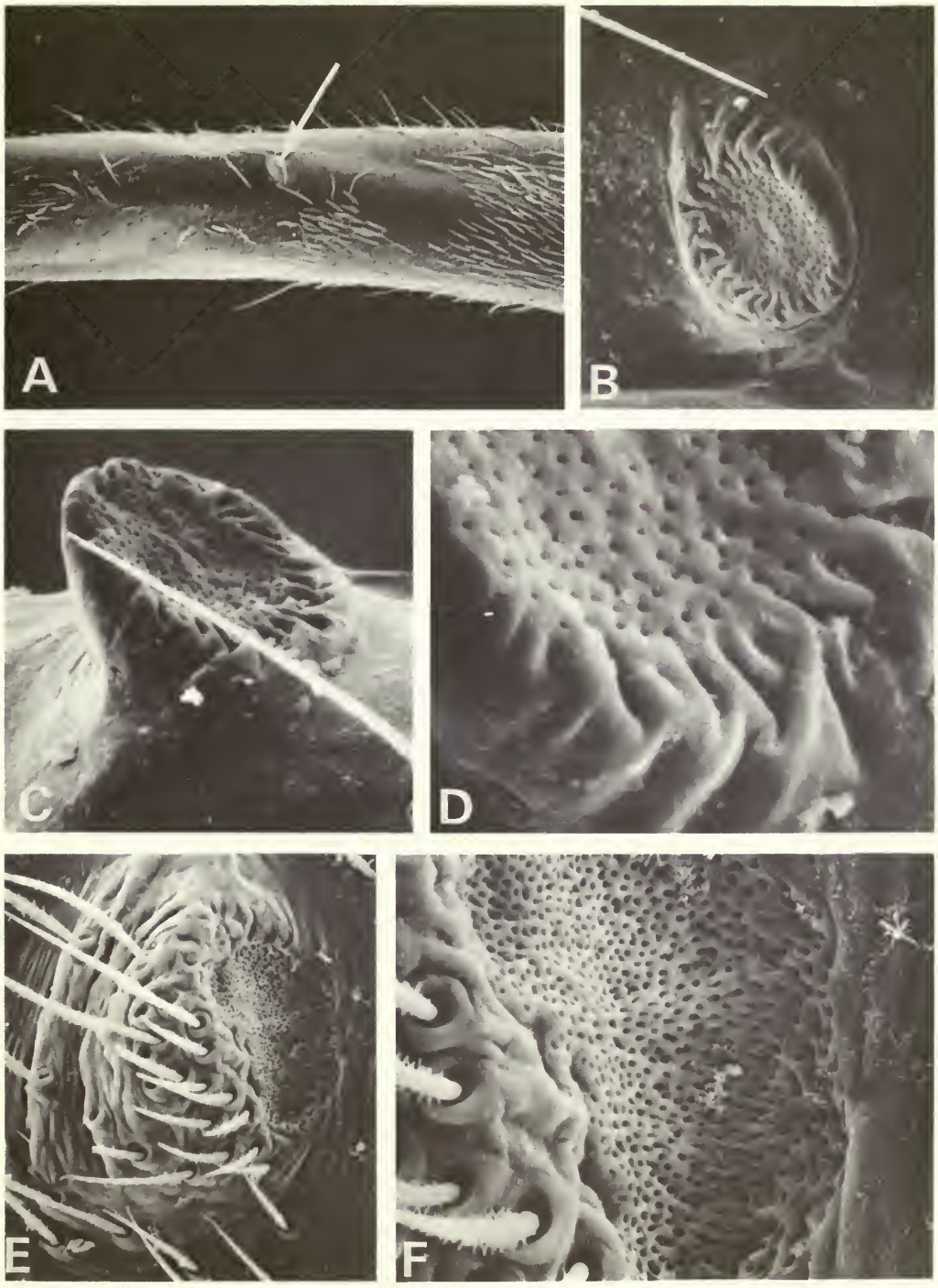

Fig. 30 (A–D) *Spartaeus spinimanus* (Thorell), ♂, femoral organ: A, femora I, ventral view (position of organ indicated by arrow) ×45; B, from above ×450; C, lateral view, ×850; D, from above, ×2000. (E–F) *Gelotia bimaculata* Thorell, ♂, femoral organ from above, ×380, ×900.

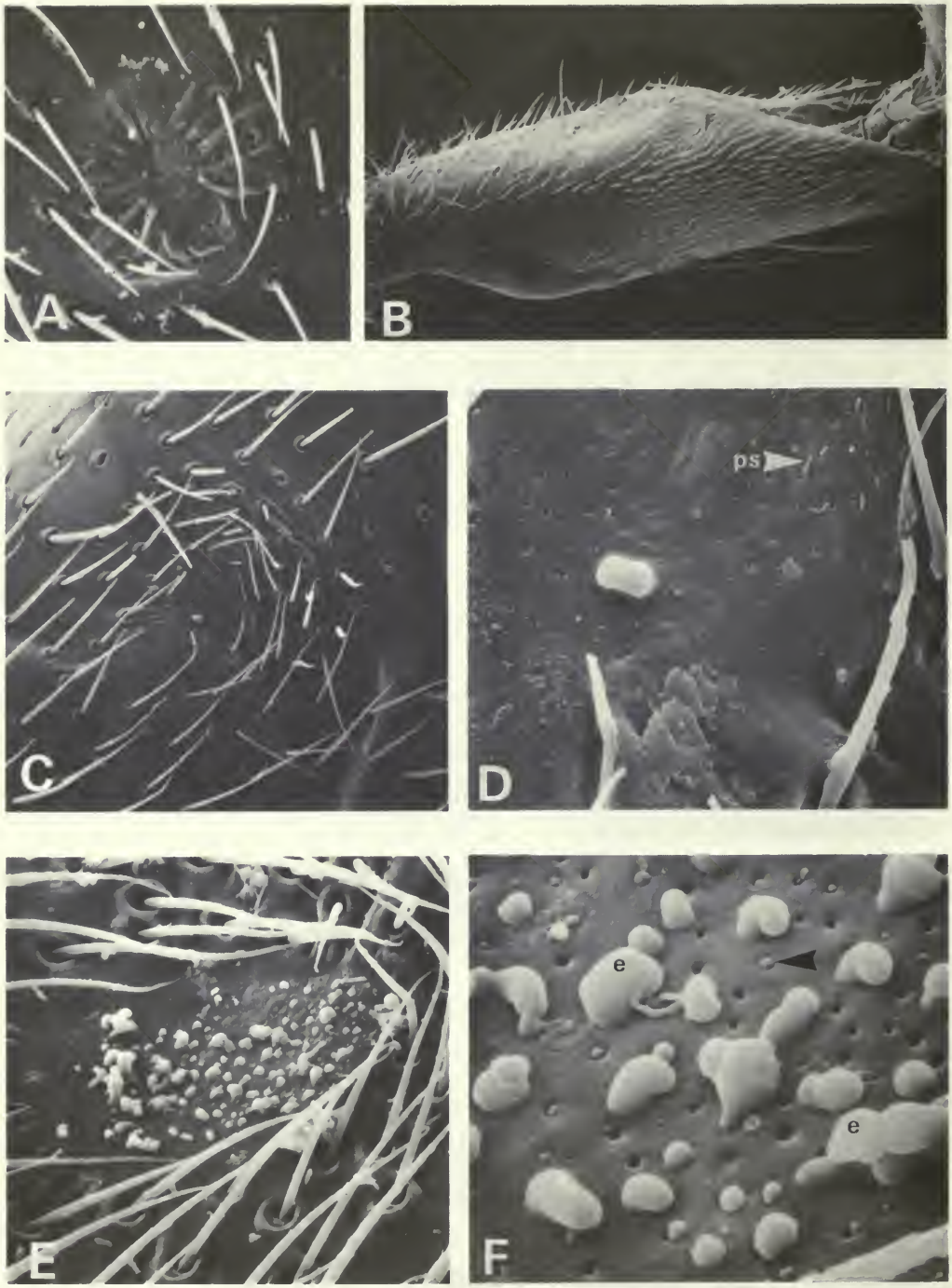

Fig. 31 *Mintonia tauricornis* sp. n., ♂, femoral organ, A, from above, ×500. (B–F) *Mintonia ramipalpis* (Thorell), ♂, femoral organ: B, femora I, ×45; C, D, from above (cleaned in ultrasonic bath) ×350; ×2100; E, F, from above (not cleaned and showing exudate) ×900, ×5000. Abbreviations: e, exudate; ps, pseudosetae.

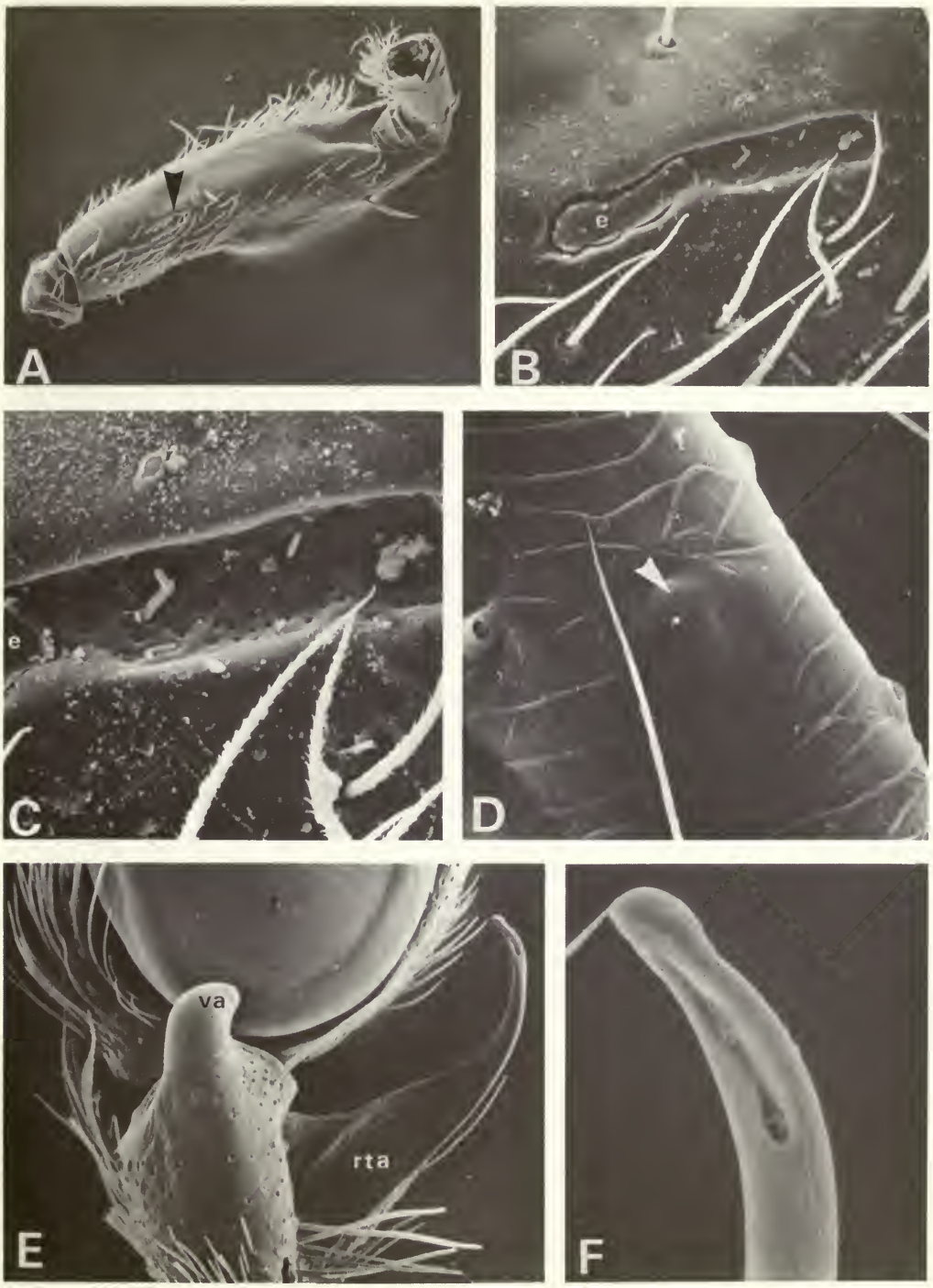

Fig. 32 (A–C) *Brettus cingulatus* Thorell, ♂: A, femora I, ventral view, ×35; B, C, femoral organ from above, ×350, ×1000. D, *Mysmena* sp., ♀, femoral organ on underside of femora II, ×900. (E–F) *Mintonia tauricornis* sp. n., ♂, palp: E, tibia from below showing oblique ventral apophysis and retrolateral apophysis, ×130; F, distal opening of retrolateral apophysis, ×800. Abbreviations: e, exudate; rta, retrolateral tibial apophysis; t, tegulum; va, ventral apophysis.

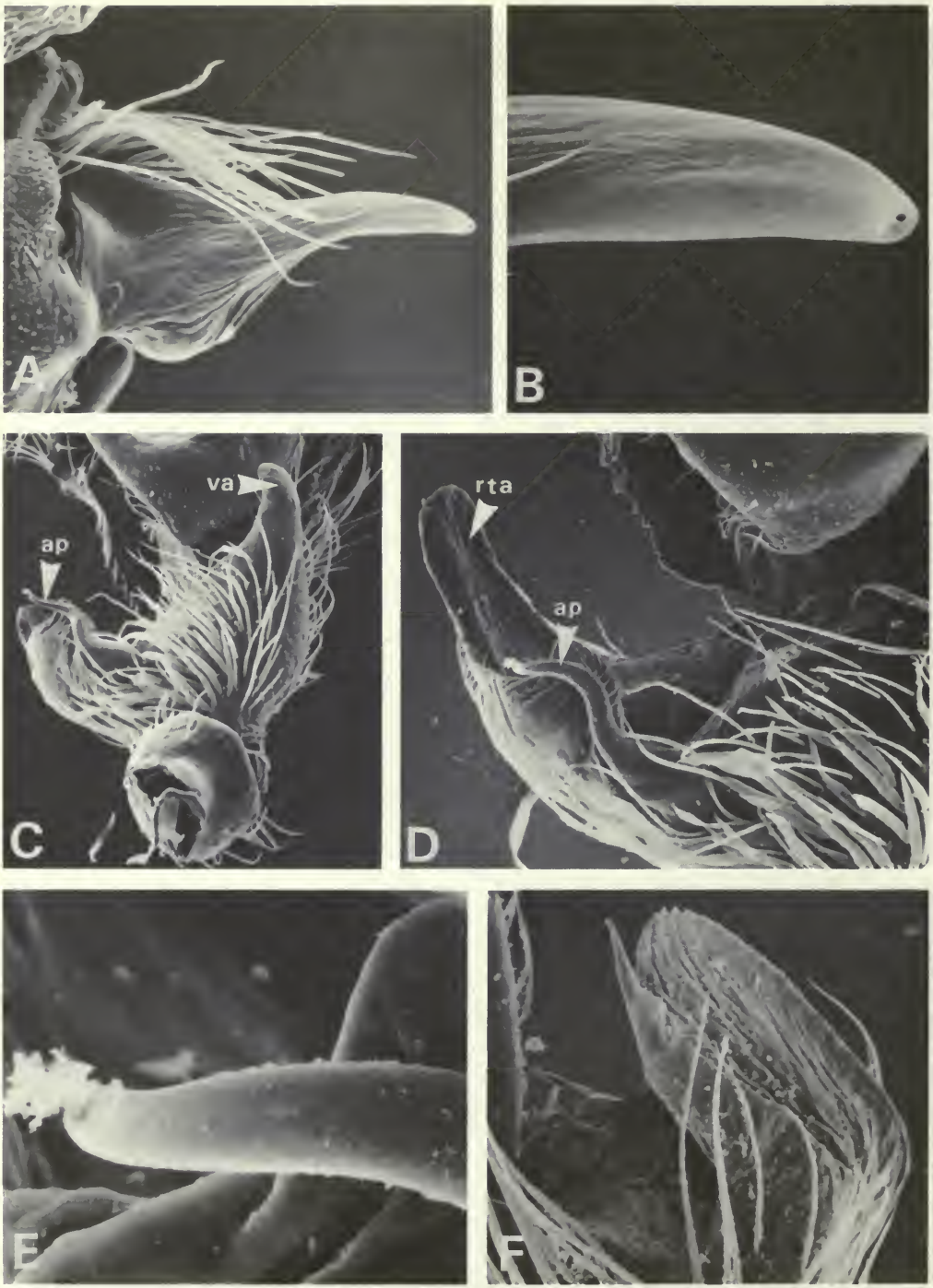

Fig. 33 (A–B) *Gelotia bimaculata* Thorell, ♂ palp: A, retrolateral tibial apophysis from below, ×120; B, distal opening of retrolateral tibial apophysis, ×400. (C–E) *Brettus cingulatus* Thorell, ♂ palp: C, showing ventral apophysis, retrolateral apophysis and adjacent tubular process, ×200; E, tubular process with distal opening partly obscured by detritus, ×2000. F, *Spartaeus spinimanus* (Thorell), ♂ palpal retrolateral tibial apophysis. Abbreviations: ap, auxillary process; rta, retrolateral tibial apophysis; va, ventral apophysis.

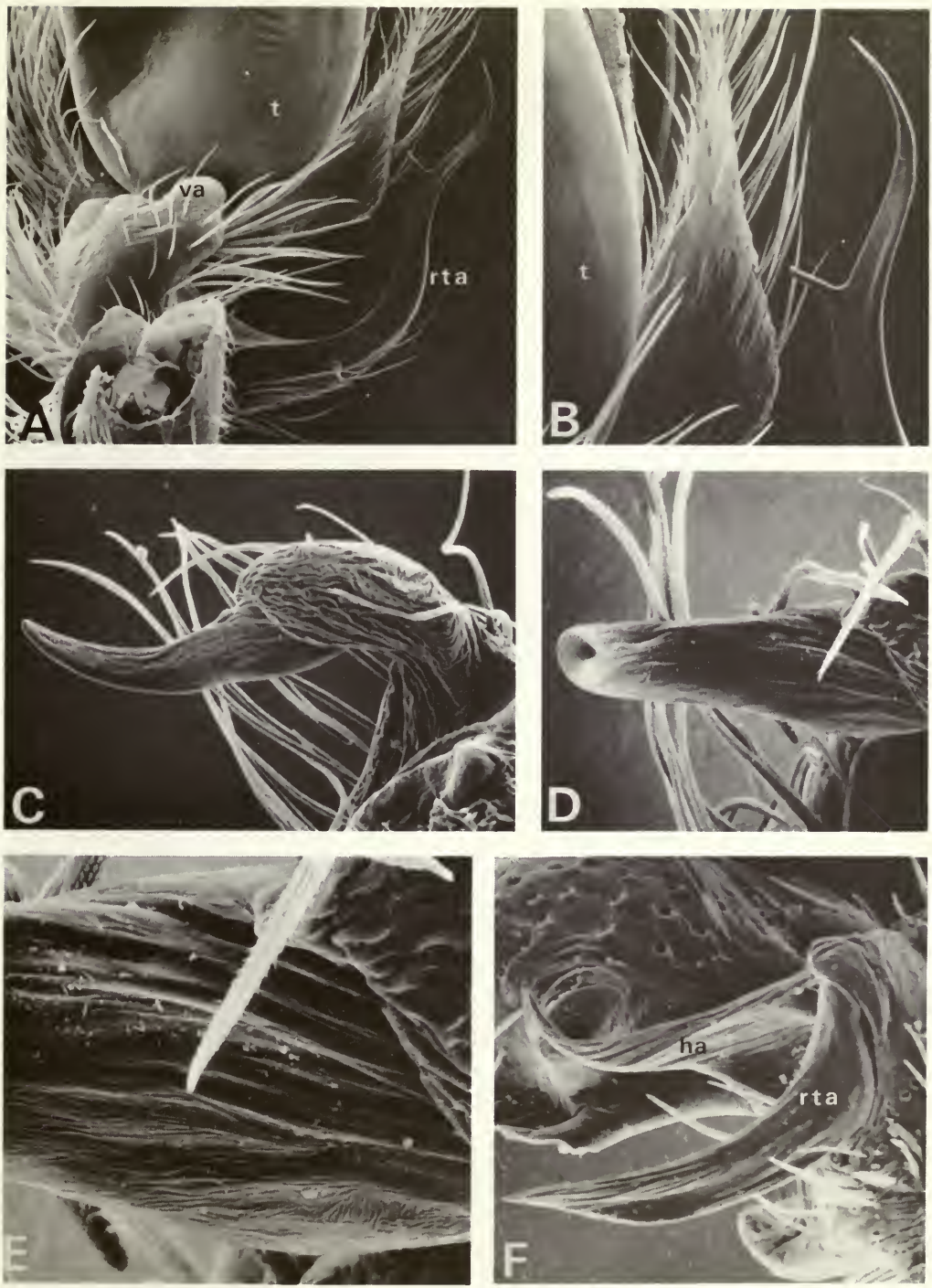

Fig. 34 (A–B) *Mintonia ramipalpis* (Thorell), ♂ palp: A, ventral and retrolateral apophyses, ×80; B, retrolateral apophyses, ×170. (C–E) *Meleon kenti* (Lessert), ♂ palp showing retrolateral tibial apophysis: C, from below, ×150; D, from in front, ×250; E, from below, ×700. F, *Cyrba algerina* (Lucas), ♂ palp, lateral view of retrolateral tibial apophysis. Abbreviations: ha, hyaline apophysis; rta, retrolateral tibial apophysis, t, tegulum; va, ventral apophysis.

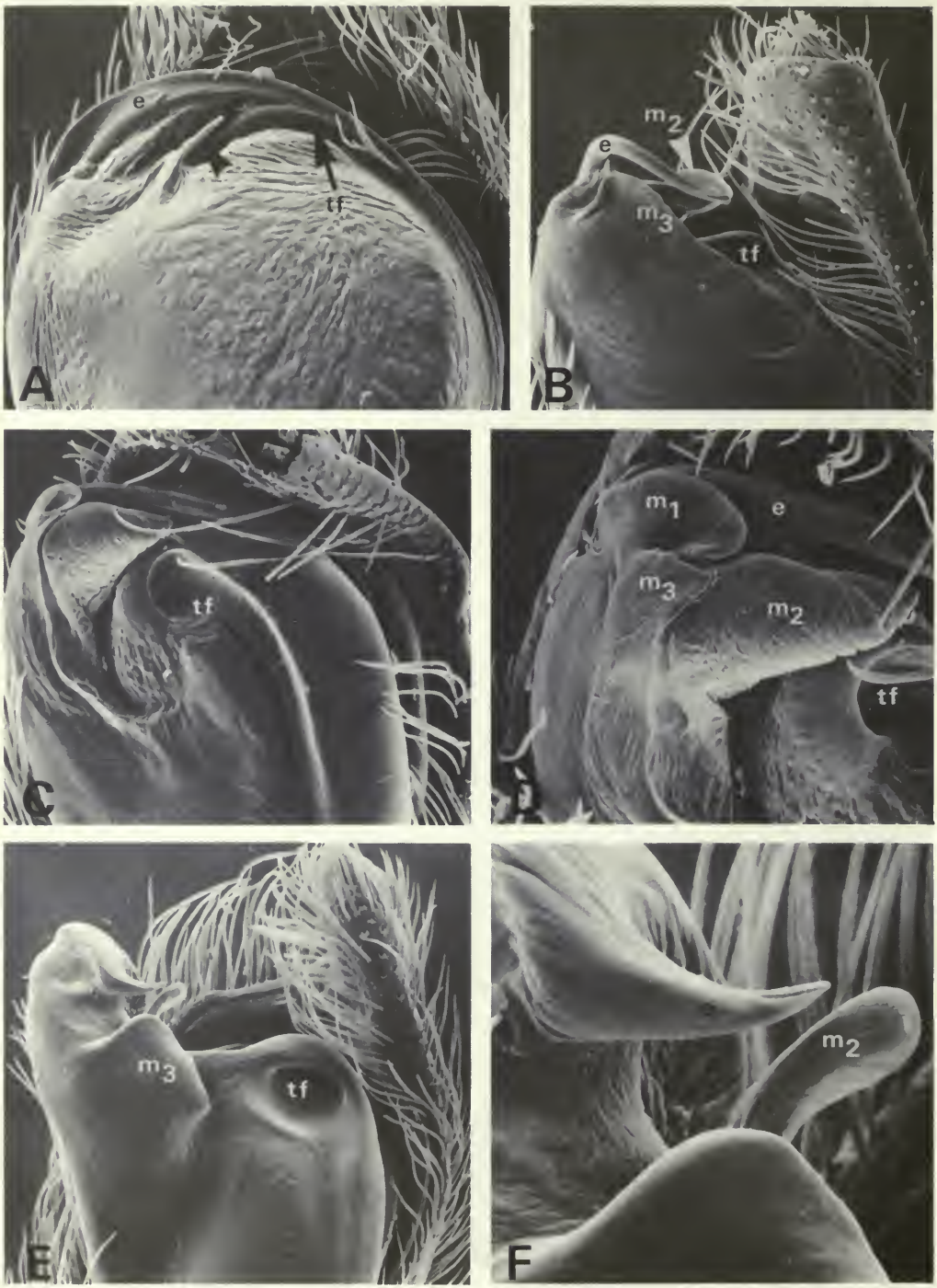

Fig. 35 (A–F) Distal region of ♂ palps, ventral view: A, *Spartaeus spinimanus* (Thorell), ×110. B, *Mintonia tauricornis* sp.n., ×100. (C–D) *Gelotia bimaculata* Thorell, ×90, ×150. (E–F) *Mintonia ramipalpis* (Thorell), ×80, ×350. Abbreviations: e, embolus; tf, tegular furrow.

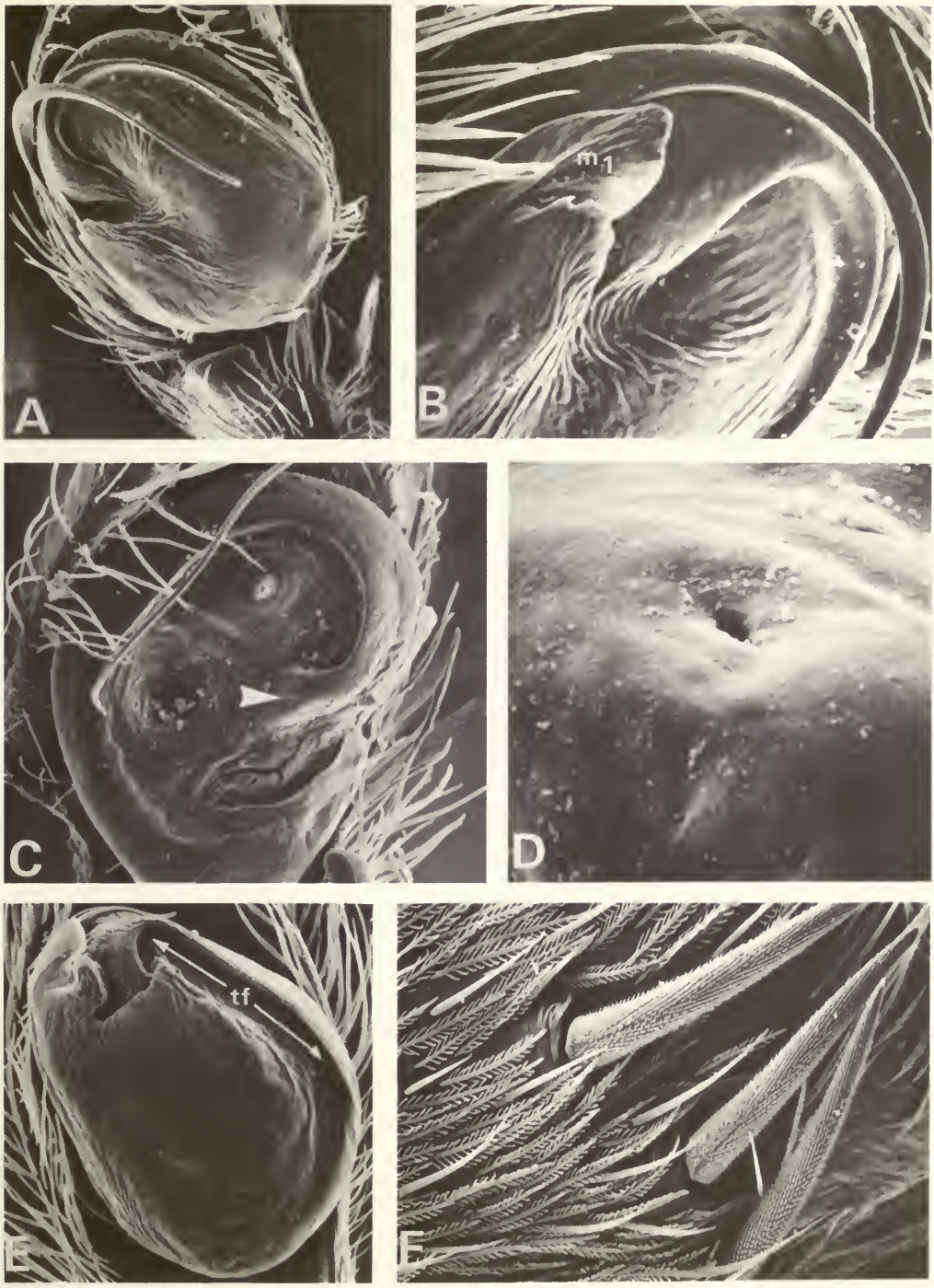

Fig. 36 (A–B) *Cyrba algerina* (Lucas), ♂ palp: ×70, ×200; (C–D) *Brettus cingulatus* Thorell, ♂ palp: C, ×150, position of pore arrowed; D, pore, ×2000. E, *Meleon kenti* (Lessert), ♂ palp showing deeply grooved furrow, ×80. F, *Mintonia ramipalpis* (Thorell), ♂ femora I showing setae and dorsal spines, ×150.

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Tilapine fishes of the genera *Sarotherodon, Oreochromis* and *Danakilia*

Dr Ethelwynn Trewavas

The tilapias are cichlid fishes of Africa and the Levant that have become the subjects of fish-farming throughout the warm countries of the world. This book described 41 recognized species in which one or both parents carry the eggs and embryos in the mouth for safety. Substrate-spawning species, of the now restricted genus *Tilapia*, are not treated here.

Three genera of the mouth-brooding species are included though in one of them, *Danakilia*, the single species is too small to warrant farming. The other two, *Sarotherodon*, with nine species, and *Oreochromis*, with thirty-one, are distinguished primarily by their breeding habits and their biogeography, supported by structural features. Each species is described. with its diagnostic features emphasised and illustrated, and to this is added a summary of known ecology and behaviour. Conclusions on relationships involve assessment of parallel and convergent evolution. Dr Trewavas writes with the interests of the fish culturists, as well as those of the taxonomists, very much in mind.

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Synopsis

One new genus and 41 new species are described in the family Nannastacidae from depths exceeding 200 m throughout the Atlantic. These are *Cumella argentinae, C. divisa, C. spinosa, C. spinoculata, C. acuminata, C. aculeata, C. echinata, C. concinna, C. exstans, C. dayae, C. subducta, C. angustata, C. erecta, C. formosa, C. bishopi, C. cristata, C. longisipho, C. spicata, C. polita, C. meridionalis, C. compacta, C. decipiens, Atlantocuma tenuis, Cumellopsis bicostata, C. laevis, Platycuma candida, Procampylaspis inermis, P. procurrens, P. lutensis, P. acanthomma, P. serratoculus, P. ommidion, P. profunda, P. hirta, Campylaspides canariensis, Campylaspis scuta, C. valida, C. gamoi, C. propinqua, C. tumulifera* and *Paracampylaspis platycarpus.* One new specific synonym and three new combinations are included. Keys are provided for identification of the deep water species of *Cumella* and the known species of *Procampylaspis.* Further records of distribution are given for another 58 species already described.

Introduction

The distribution of 39 species of the genus *Campylaspis* and description of 25 new species among them were recorded in Jones (1974) and two new species of *Platycuma* and one of *Campylaspides* described in Jones (1973). Two of the supposed new species of *Campylaspis* are now considered to be synonymous with previously described species.

In the present paper records of distribution additional to those in Jones (1973, 1974) are given for all the species in the family Nannastacidae found in the collections so far examined and a further 41 new species are described. In all, 99 nannastacid species found in depths

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Fig. 1 The Atlantic Ocean, showing areas from which Cumacea included in this report have been collected. Solid black circles show approximate localities of one or several stations.

exceeding 200 m throughout the Atlantic are included, while no further specimens were found of another 14 species of *Campylaspis* described in Jones (1974). Thus 59% of the total nannastacid species found among the material from the collections listed below were previously undescribed. This is probably typical, within a few per cent, of the other cumacean families.

Descriptions and records of some of the species in other families from the same collections are given in Jones (1973), Reyss (1974*a*, 1974*b*, 1975, 1978*a*, 1978*b*) and Bishop (1980, 1981*a*, 1918*b*, 1982). A preliminary account of distribution of cumacean species in the deep Atlantic was given by Jones and Sanders (1972). No general comments on distribution will be made here but it is hoped that these will be published elsewhere.

In the descriptions that follow, length of individuals is measured from the tip of the pseudorostrum (excluding siphons) to the end of the pleon (excluding uropods).

Station details

The general location of the stations at depths of 200 m or more from which material containing species of the Nannastacidae was examined is shown in Fig. 1. The sectors of the Atlantic covered by the various cruises are outlined below; full station details have been deposited in the Crustacea Section, British Museum (Natural History). The abbreviation MBAUK refers to the Marine Biological Association of the United Kingdom, Plymouth; IOS, Institute of Oceanographic Sciences, Wormley; SMBA, Scottish Marine Biological Association, Dunstaffnage; SBR, Station Biologique de Roscoff; COB, Centre Océanologique de Bretagne, Brest; WHOI, Woods Hole Oceanographic Institution.

Ship and/or Cruise (Institution)	No. of stations with Nannastacidae examined	Date	Latitude	Longitude	Depth range/m
Sarsia (MBAUK)	8	1967	43° 35.6′ – 47° 40′ N	3° 24.8′ – 5° 0′ W	119–2379
Discovery II (IOS)	7	1968	27° 13′ – 28° 06′ N	13° 28′ – 15° 41′ W	1780–3301
Discovery II (IOS)	5	1971	59° 56.6′ – 60° 08.3′ N	19° 24.8′ – 20° 00.1′ W	2636–2714
Challenger (SMBA)	12	1973	54° 40′ – 56° 52′ N	09° 10′ – 12° 33′ W	704–2900
Challenger (SMBA)	10	1976,1977, 1978	54° 34′ – 56° 39′ N	09° 13′ – 12° 29′ W	1000–2921
Thalassa 70 (SBR)	2	1970	43° 36.2′ – 43° 41.1′ N	02° 17′ – 03° 49.8′ W	320–1050
Thalassa 72 (SBR)	1	1972	41° 30.7′ N	09° 19.9′ W	1250
Thalassa 73 (SMB)	40	1973	47° 33.4′ – 48° 56′ N	07° 16.8′ – 11° 14.3′ W	330–2070
La Perle BIOGAS I (COB)	10	1972	47° 27′ – 47° 56.5′ N	07° 40.1′ – 08° 39.9′ W	400–2210
Jean Charcot POLYGAS (COB)	11	1972	44° 08.2′ – 47° 36.1′ N	04° 15′ – 10° 21′ W	2076–4734
Jean Charcot BIOGAS II, III, IV, VI (COB)	31	1973, 1974	44° 04′ – 47° 42.4′ N	04° 15.4′ – 10° 27.1′ W	1031–4715
Cryos BIOGAS V (COB)	3	1974	47° 28.2′ – 47° 36.1′ N	08° 40.5′ – 09° 35′ W	2360–4150

Ship and/or Cruise (Institution)	No. of stations with Nannastacidae examined	Date	Latitude	Longitude	Depth range/m
Jean Charcot NORBI (COB)	1	1975	69° 52.1′ N	17° 08.5′ E	300
Atlantis 255, 264, 273, 277, 283, 284	40	1960, 61 62, 64 65, 66 69, 73.	31° 19′ – 39° 58.4′N	64° 36.3′ – 71° 47′ N	300– 5007
Atlantis II 12, 17, 23, 24, 30, 40 **Chain** 50, 58, 88 **Knorr** 35 (WHOI)		65, 66, 69, 73.			
Chain 35 (WHOI)	1	1963	07° 08′ S	34° 25·5′ W	770– 805
Atlantis II 31 (WHOI)	8	1967	10° 30′ N– 08° 02′ S	17° 49′ – 34° 25′ W	587– 3783
Atlantis II 42 (WHOI)	12	1968	08° 46′ – 22° 54′ S	09° 04′ – 13° 32′ E	205– 4566
Atlantis II 59 (WHOI)	2	1970	33° 40′ – 33° 57′ N	15° 08·2′ – 16° 16′ E	500– 1509
Atlantis II 60 (WHOI)	14	1971	36° 05.2′ – 38° 16.9′ S	48° 58.1′ – 53° 23.9′ W	256– 5223
Knorr 25 (WHOI)	10	1972	07° 45.3′ – 13° 16′ N	52° 24′ – 56° 20′ W	508– 4980
Chain 106 (WHOI)	6	1972	50° 04.7′ – 51° 32.2′ N	12° 35.9′ – 15° 44.8′ W	1491– 4435
Chain 106 (WHOI)	1	1972	40° 42.6′ – 40° 44′ N	46° 13.8′ – 46° 14.6′ W	4400

Systematic descriptions and details of distribution

Genus *CUMELLA* Sars, 1865

No eyes or a single median ocular group. Maxilliped 2 usually with 6 segments. Peduncle of the uropods usually longer than the rami and the inner ramus usually longer than the outer.

Bacescu (1972) erected a new genus, *Schizocuma,* with the following diagnosis: pseudorostral lobes widely separated, forming two divergent funnels slightly upraised. Frontal lobes huge, terminating in the optic lobe without any trace of lenses. Abdominal segments and uropods particularly long and thin. Basis of maxilliped 3 without lower anterior projection and basis of pereopod hardly broadened proximally. He included in the genus a new species *S. vemae* and *Schizotrema calmani* Stebbing, 1912, together with *Cumella molossa* Zimmer, 1907.

Bacescu and Muradian (1974*a*) erected a further new genus, *Styloptocuma,* to include a new species, *S. antipai,* with *Cumella gracillima* Calman, 1905, and *C. egregia* Hansen, 1920. The generic diagnosis was: very elongated cumaceans, richly provided with spines at least on the carapace. Long pseudorostrum suddenly curved, considerably overrun in length by an aberrant ocular styliform lobe, without any trace of visual elements. Antenna 1 with a very long basal segment, exceeding the whole length of the appendage. Pereopods and uropods extremely long.

No clear pattern emerges among the new species described here by which they can be separated into genera. Three of the new species have a partially divided eyelobe as in

Schizocuma vemae and although they have separated siphons, these are set close together and not widely separated. The pleon and uropods are not particularly long and thin in these species and they do not differ in these respects from other species with undivided eyelobes. *Cumella carinata* (Hansen, 1887) has a partially divided eyelobe but could not possibly be placed in *Schizocuma.* Stebbing's *Schizotrema calmani* apparently does not have a divided eyelobe although he states that the pseudorostral lobes are widely apart in dorsal aspect. Although this species obviously does not belong to *Schizotrema,* it also has little in common with *Schizocuma vemae. Cumella molossa* shows equally little resemblance to *Schizocuma vemae* but does resemble *Cumella spinoculata* sp. n. described below.

Styloptocuma antipai quite closely resembles *Cumella egregia* but less closely *Cumella gracillima.* However, some of the other species described below are close to one or other of these three species but are not sharply separated from others. I do not propose to accept *Schizocuma* or *Styloptocuma* as valid genera. The shape of the eyelobe varies greatly in *Cumella* but no obvious grouping can be seen in this character. There may, however, be a case for dividing the genus into the shallow water species with well developed but not elongated eyelobe with lenses distinct, fairly short and compact carapace and pereon, and relatively short uropods, from the remainder found in deeper water, with the eyelobe rudimentary or elongated but without lenses, carapace and pereon often more elongated, and uropods relatively long. Even among the species so far known, and there must be many as yet undescribed, the division breaks down in several instances. I propose, therefore, to refer all the species to *Cumella* for the present.

The following descriptions are mainly confined to those characters which can be examined under a stereoscopic microscope. In the genus *Cumella* the mouthparts do not show much variation, and the important characters for identification are the proportions and armature of the carapace, the relative length of the pseudorostrum and the angle which it makes with the dorsal line of the carapace, the length, shape and armature of the eyelobe and presence or absence of visual elements, the proportions and shape of the first antenna and to a lesser extent the anterior pereopods, the armature of the pereon, the relative length and slenderness of the pleon and the presence, number or absence of spine rows or serrations on it, and the relative length, proportions and armature of the uropods.

Cumella argentinae sp. nov.
(Fig. 2)

MATERIAL. AII60–280: 1 imm. ♂, 10 ad. ♀♀, 7 juv.

DESCRIPTION. Ovigerous female, length 2·7 mm: carapace (Fig. 2a–c) more than 1½ as long as deep, rather compressed laterally, with usually some short setae and a distinct dorsal ridge bearing a series of more than 30 small teeth diminishing in size from front to rear, but these are not developed in some individuals; the pseudorostrum is fairly short and the siphons not very long; the antero-lateral angle is fairly prominent with a row of serrations extending backwards from it; the eyelobe is broad and well developed, with lenses visible. Pereon and pleon without spines, the pleon a little shorter than the carapace and pereon combined.

Antenna 1 (Fig. 2d) short with basal segment about as long as second and third together, the second with a blunt distal projection. Pereopod 1 (Fig. 2g) with basis a little shorter than remaining segments together; there are some blunt serrations along its lower distal edge; the carpus is about twice as long as the propodus and three times as long as the dactyl. Pereopod 2 (Fig. 2h) with basis broad, some serrations on its upper distal edge, nearly as long as remaining segments together; its dactyl is fairly broad, about as long as the carpus and propodus together. Uropod (Fig. 2i) with peduncle not very long, about as long as pleonite 5 and 1½ as long as the endopod, which is distinctly longer than exopod; the peduncle is serrated on the inner edge and the endopod has a few longer spines interspersed with more short spines.

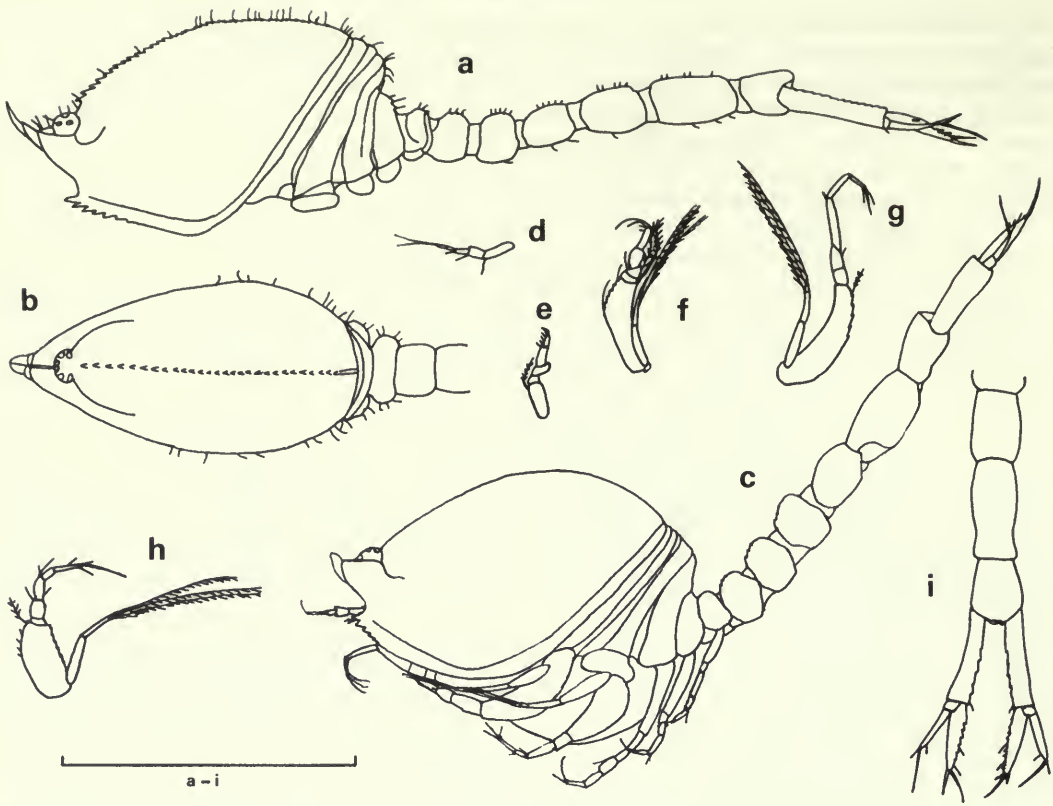

Fig. 2 *Cumella argentinae* ♀, (a) lateral view; (b) carapace and pereon from above; (c) ovigerous ♀ from side; (d) antenna 1; (e) maxilliped 2; (f) maxilliped 3; (g) pereopod 1; (h) pereopod 2; (i) uropods and end of pleon. Scale bars in this and the following figures represent 1 mm.

TYPE LOCALITY. 36° 18′ S, 53° 23.9′ W, 256–293 m. Types deposited in the British Museum (Natural History). Holotype 1982 : 292 : 1, paratypes 1982 : 293 : 5.

REMARKS. *C. argentinae* quite closely resembles *C. pygmaea* Sars but the female carapace is either smooth or has about 30 small teeth dorsally rather than having not more than 12 longer mid-dorsal spines.

DISTRIBUTION. Although it was collected from somewhat below 200 m depth, it is probably a shelf species as suggested by the well developed eye.

Found so far only off the Argentine coast in 256–293 m.

Cumella tarda Hansen 1920
(Fig. 3)

MATERIAL. SMBA-ES 129: 1 ad. ♂. *Thalassa* 73-Z426: 1 ad. ♂.

DISTRIBUTION. Although the two hauls from which single specimens were obtained took place in depths of 860 and 2900 m respectively from Biscay and west of Scotland, Hansen's original records were from a pelagic haul south-west of the Faroes. The facts that only adult males have been collected and these have well developed eyes with large lenses make it likely that these two specimens entered the nets near the surface on the way up or down, although the whereabouts of the females remain unknown.

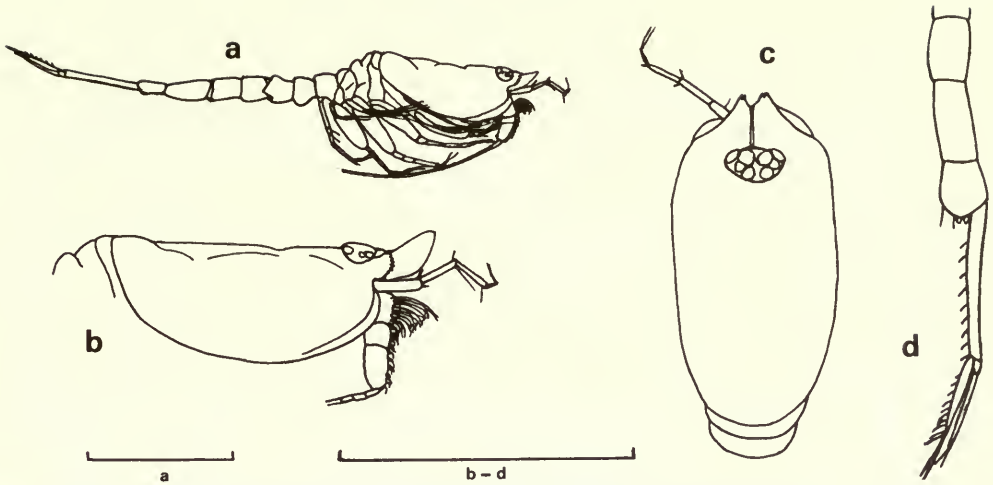

Fig. 3 *Cumella tarda* ♂, (a) lateral view (flagellum of antenna 2 incomplete); (b) carapace from side; (c) carapace from above; (d) uropod and end of pleon.

Cumella gracillima Calman, 1905
(Fig. 4)

MATERIAL. MBAUK-50: 1 imm. ♀. SMBA-ES4: 2 imm. ♀♀. ES12: 2 ad. ♀♀, 2 imm. ♀♀. ES22: 5 ad. ♂♂, 8 ad, ♀♀, 1 juv. ES147: 1 ad. ♂, 1 imm. ♂, 3 ad. ♀♀. *Thalassa* 70-W357: 4 ad. ♀♀. *Thalassa* 73-Z434: 1 ad. ♀. Z457: 2 imm. ♀♀. BIOGAS I-DS08: 1 imm. ♀. DS11: 1juv. DS13: 1 ad. ♂, 1 imm. ♂, 2 ad. ♀♀. POLYGAS-DS15: 5 ad. ♂♂, 10 imm. ♂♂, 30 ad. ♀♀, 6 imm. ♀♀. DS18: 1 ad. ♂, 6 imm. ♂♂, 10 ad. ♀♀, 10 imm. ♀♀. BIOGAS III-DS35: 1 imm. ♂, 3 ad. ♀♀. DS41: 2 imm. ♀♀. BIOGAS IV-DS64: 2 imm. ♀♀. BIOGAS V-DS66: 3 imm. ♀♀. BIOGAS VI-CP09: 2 imm. ♂♂, 5 imm. ♀♀. CP25: 1 ad. ♀, 1 imm. ♀. AII12–64: 1 ad. ♂, 22 ad. ♀♀, 3 imm. ♀♀. 66: 8 ad. ♀♀, 4 juv. 72: 1 imm. ♂. Ch50-85: 4 imm. ♂♂, 8 ad. ♀♀. 87: 1 ad. ♀. AII17-95: 2 juv. AII31-155: 1 ad. ♂, 2 imm. ♂♂, 2 ad. ♀♀, 2 imm. ♀♀. 156: 5 imm. ♂♂. 159: 1 ad. ♂, 1 imm. ♂, 2 ad. ♀♀. AII42-200: 1 imm. ♂, 2 juv. AII60-239: 3 imm. ♀♀ Kn25-287: 1 imm. ♂, 2 ad. ♀♀, 3 imm. ♀♀, 1 juv. 288: 2 imm. ♂♂, 2 ad. ♀♀, 2 imm. ♀♀. 291: 3 ad. ♀♀. 293: 2 ad. ♀♀, 1 imm. ♀. 299: 3 ad. ♀♀, 3 imm. ♀♀. 301: 25 imm. ♂♂, 27 ad. ♀♀, 22 imm. ♀♀. 303: 14 imm. ♂♂, 25 ad. ♀♀, 7 juv. 306: 1 ad. ♀. Ch106-313: 2 ad. ♀♀, 2 juv. 321: 1 imm. ♀. 334: 3 imm. ♂♂, 5 imm. ♀♀, 1 juv. Kn35-340: 4 ad. ♂♂, 16 imm. ♂♂, 18 ad. ♀♀, 15 imm. ♀♀, 7 juv.

DISTRIBUTION. Previously recorded only from west of Ireland, 364–699 m., this species is widespread throughout the deep Atlantic down to 5000 m and especially on the lower slope and in abyssal depths.

Cumella egregia Hansen, 1920
(Fig. 5)

MATERIAL. MBAUK-65: 1 ad. ♀. IOS-6711: 1 ad. ♀. SMBA-ES4: 1 imm. ♂, 1 imm. ♀. BIOGAS I-DS05: 1 ad. ♂. DS13: 5 imm. ♂♂, 2 ad. ♀♀, 1 juv. POLYGAS-DS15: 5 imm. ♂♂, 21 ad. ♀♀, 5 imm. ♀♀. DS16: 3 ad. ♀♀. DS17: 4 ad. ♀♀. DS18: 1 ad. ♂, 1 imm. ♂, 9 ad. ♀♀, 20 imm. ♀♀. BIOGAS II-DS31: 1 ad. ♂, 1 imm. ♂, 3 imm. ♀♀. BIOGAS III-DS36: 1 imm. ♀. DS41: 1 ad. ♂, 8 imm. ♂♂, 7 ad. ♀♀, 2 imm. ♀♀. BIOGAS IV-DS64: 2 ad. ♂♂. BIOGAS V-DS65: 1 ad. ♀. BIOGAS VI-CP23: 4 ad. ♀♀. CP24: 2 imm. ♂♂, 1 ad. ♀. Ch50-85: 3 ad. ♂♂, 9 imm. ♂♂, 9 ad. ♀♀. AII24-126: 2 ad. ♀♀. AII31-156: 1 imm. ♂, 1 imm. ♀. 159: 1 imm. ♂. 167: 1 imm. ♂, 4 ad. ♀♀, 1 imm. ♀. 169: 3 imm. ♂♂, 1 ad. ♀. Kn25-287: 1 imm. ♂, 3 ad. ♀♀, 1 imm. ♀. 295: 2 imm. ♂♂, 10 ad. ♀♀, 3 juv. 299: 1 ad. ♂, 3 imm. ♂♂, 8 ad. ♀♀. 301: 2 imm. ♂♂. Ch106-334: 1 imm. ♂, 1 imm. ♀.

DISTRIBUTION. Previous records were only those of Hansen from the Davis Strait in 2624 m. The present records show it to be widespread between 587 and 4400 m, with much the same distribution in the North Atlantic as *C. gracillima*. There are no records yet from the South Atlantic south of the tropics.

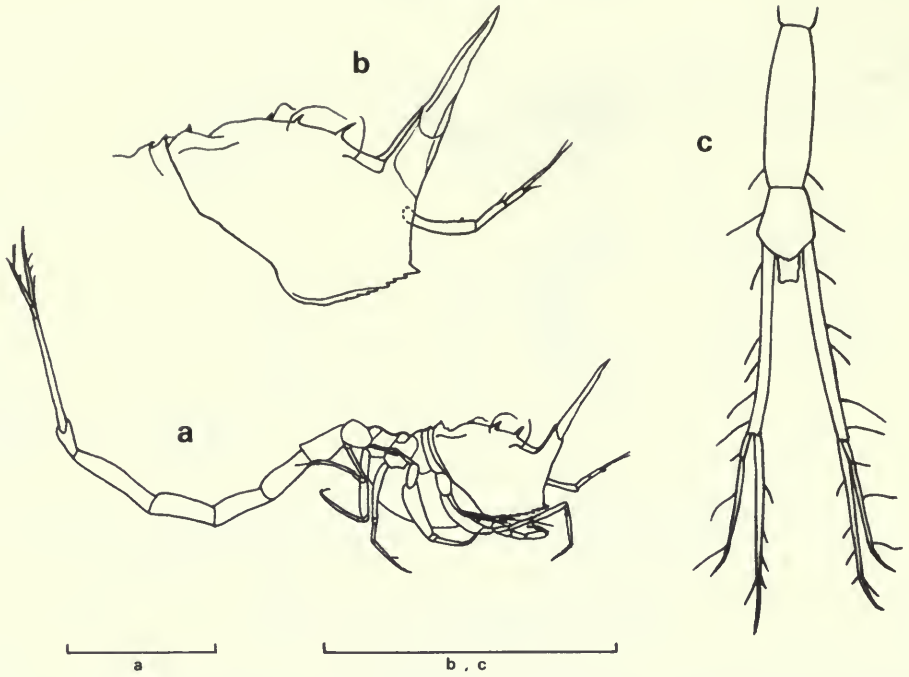

Fig. 4 *Cumella gracillima* ovigerous ♀, (a) lateral view; (b) carapace from side; (c) uropods and end of pleon.

Cumella antipai (Bacescu & Muradian, 1974) comb. nov.
(Fig. 6)

Styloptocuma antipai Bacescu & Muradian, 1974.

MATERIAL. Kn25-293: 12 ad. ♀♀, 5 imm. ♀♀.

DISTRIBUTION. The original records were from Cape Hatteras to Florida, 1000 to 1091 m. It is now recorded from 1500 m off Surinam.

Cumella vemae (Bacescu, 1972) comb. nov.
(Fig. 7)

Schizocuma vemae Bacescu, 1972.

MATERIAL. BIOGAS I-DS05: 2 ad. ♀♀, 2 imm. ♀♀, 3 juv. DS06: 1 ad. ♂, 1 ad. ♀. DS07: 3 imm. ♂♂. DS11: 3 imm. ♀♀. DS13: 1 imm. ♂, 4 ad. ♀♀, 1 juv. POLYGAS-DS15: 7 imm. ♂♂, 13 ad. ♀♀. DS16: 1 imm. ♂, 1 imm. ♀. DS18: 3 ad. ♂♂, 4 imm. ♂♂, 24 ad. ♀♀, 20 imm. ♀♀. DS26: 1 imm. ♀. BIOGAS II-DS32: 1 imm. ♂. BIOGAS III-DS35: 2 ad. ♀♀, 2 imm. ♀♀. DS36: 1 imm. ♀. DS37: 1 imm. ♀, 1 juv. DS38: 1 imm. ♀, 2 juv. DS49: 1 imm. ♀. BIOGAS IV-DS62: 2 imm. ♀♀, 1 juv. DS63: 1 imm. ♂, 2 imm. ♀♀. DS64: 1 ad. ♂, 1 imm. ♂, 4 ad. ♀♀, 6 imm. ♀♀. BIOGAS VI-DS86: 1 imm. ♂, 7 ad. ♀♀, 4 imm. ♀♀, 1 juv. DS87: 1 ad. ♂, 1 imm. ♂, 4 ad. ♀♀, 10 imm. ♀♀. CP09: 1 imm. ♀. CP23: 1 imm. ♂, 3 ad. ♀♀, 1 imm. ♀. CP24: 1 imm. ♂. CP25: 2 imm. ♂♂, 3 ad. ♀♀, 2 imm. ♀♀. AII31-167: 3 imm. ♂♂, 1 ad. ♀. Kn25–297: 1 imm. ♂.

DISTRIBUTION. Known previously from a single male, east of Florida, 1316 m, it is now recorded from the Bay of Biscay and off the coasts of tropical Brazil and Surinam, from the slope between 500 and 2350 m. The adult female (Fig. 7a, b) has a series of about four prominent spines mid-dorsally on the carapace.

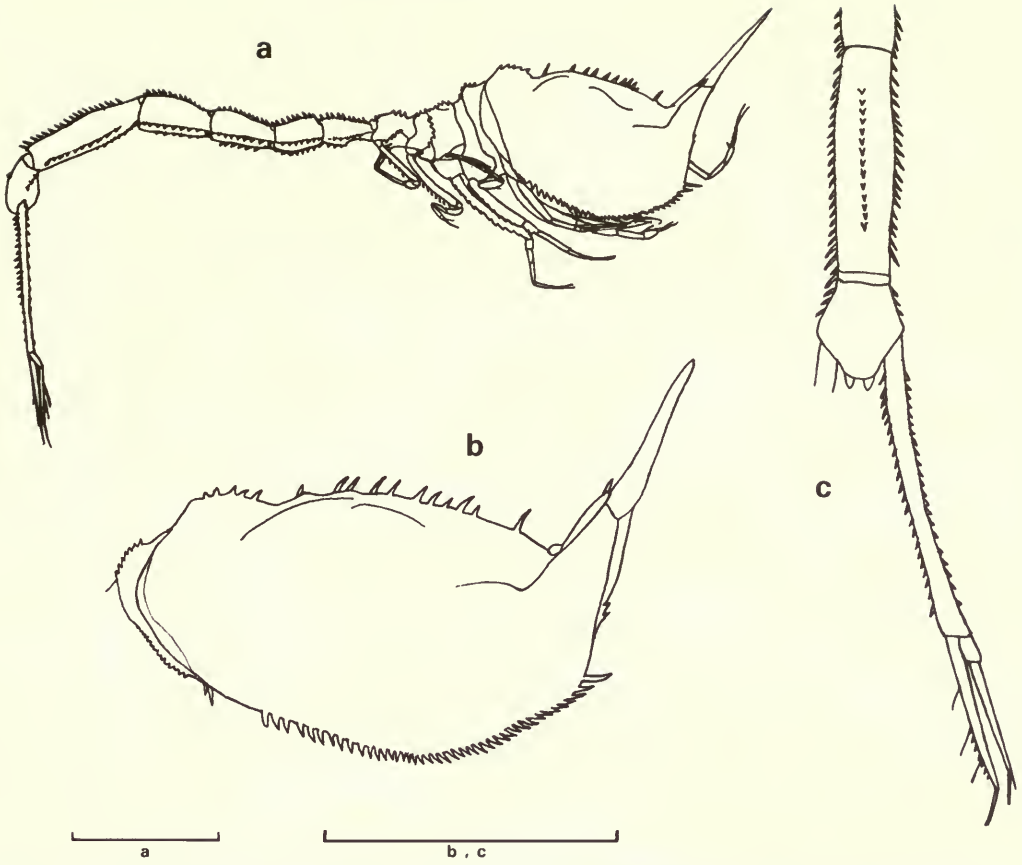

Fig. 5 *Cumella egregia* ♀, (a) lateral view; (b) carapace from side; (c) uropod and end of pleon.

Cumella divisa sp. nov.
(Fig. 8)

MATERIAL. MBAUK-65: 1 imm. ♂, 1 juv. SMBA-ES10: 3 imm. ♂♂, 1 ad. ♀. ES18: 1 ad. ♀, 1 imm. ♀. ES20: 1 ad. ♀, 1 imm. ♀, 1 juv. *Thalassa* 73-Z413: 2 imm. ♀♀. Z421: 1 ad. ♀. Z429: 1 imm. ♂, 1 ad. ♀, 4 imm. ♀♀. Z435: 1 imm. ♂, 1 imm. ♀. Z437: 1 ad. ♀, 2 imm. ♀♀. Z438: 3 imm. ♂♂, 3 imm. ♀♀. Z445: 1 imm. ♂. Z447: 1 imm. ♂, 4 ad. ♀♀, 2 imm. ♀♀. Z449: 1 imm. ♀. Z453: 1 imm. ♀, 1 juv. BIOGAS I-DS05: 1 ad. ♀. DS09: 1 imm. ♂. DS13: 1 ad. ♀. BIOGAS IV-DS51: 1 imm. ♂, 1 ad. ♀. AII31-142: 2 imm. ♂♂, 3 ad. ♀♀. AII42-192: 1 ad. ♀. 194: 1 imm. ♀. Ch106-318: 2 imm. ♀♀.

DESCRIPTION. Adult female, length 3·0 mm: carapace (Fig. 8a, b) rather long, twice as long as high, with a short pseudorostrum little upturned. Siphon fairly long. Dorsal outline somewhat uneven, without spines except on the eyelobe but with some scattered hairs. The eyelobe is not elongated but broad and distinctly doubled and seems to show the rudiments of lenses. Antero-lateral angle marked by a prominent tooth with the border serrated behind. Pereon somites unarmed except for a few hairs. Pleon fairly short, without spines or setae. Pleonite 6 little produced backwards and truncate posteriorly.

Antenna 1 fairly long but basal segment shorter than second and third together, the second without a distal projection. Pereopod 1 (Fig. 8c) with basis about half length of rest of appendage; propodus about $1\frac{1}{2}$ as long as carpus and more than twice as long as dactyl. Pereopod 2 (Fig. 8d) with basis about 4/5 length of rest of appendage; dactyl distinctly longer than carpus and more than twice as long as propodus. Pereopod 5 of normal length. Uropod

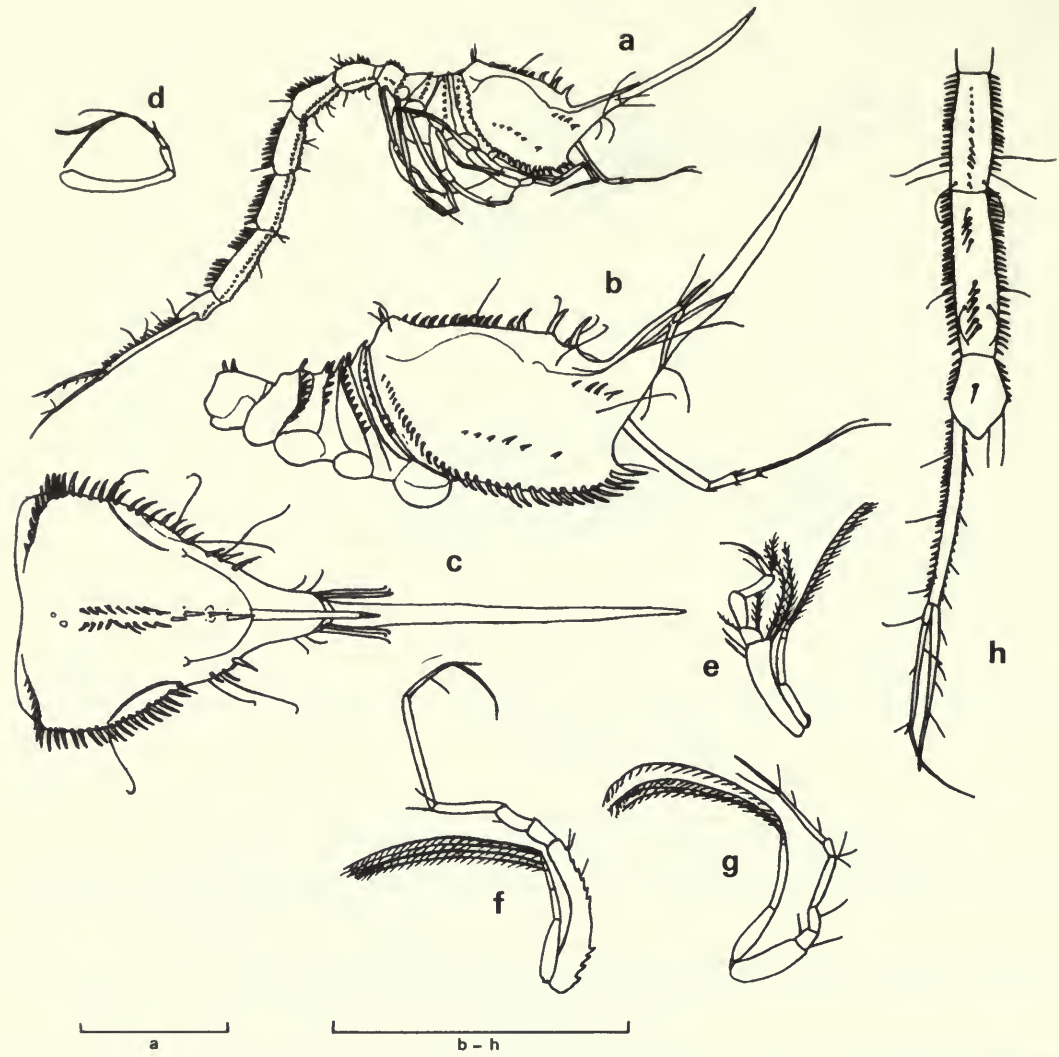

Fig. 6 *Cumella antipai* ovigerous ♀, (a) lateral view; (b) carapace and pereon from side; (c) carapace from above; (d) antenna 1; (e) maxilliped 3; (f) pereopod 1; (g) pereopod 2; (h) uropod and end of pleon.

(Fig. 8e) fairly long, with peduncle unarmed except for about 7 setae, shorter than last two pleonites together and about $1\frac{1}{2}$ as long as the endopod, which is little longer than the exopod.

TYPE LOCALITY. 48° 47.3′ N–48° 47.4′ N, 11° 12′ W–11° 14.3′ W, 1430–1550 m. Type specimens deposited in the Museum National d'Histoire Naturelle, Paris. Holotype ♀ no. Cu 198, paratypes Cu 199.

REMARKS. This and the following two species have the eyelobe divided into two parts but differ from *Cumella vemae* in having the pseudorostral lobes and siphons either together or only narrowly separated and by having a prominent spine on each half of the eyelobe. From *C. spinosa* sp. nov. it is easily distinguished, at least in the female, by the absence of dorsal spines on the carapace and from *C. spinoculata* sp. nov. by the absence of spines below the pseudorostrum, the less prominent antero-lateral angle of the carapace and the lack of spine rows transversely on the pereon somites.

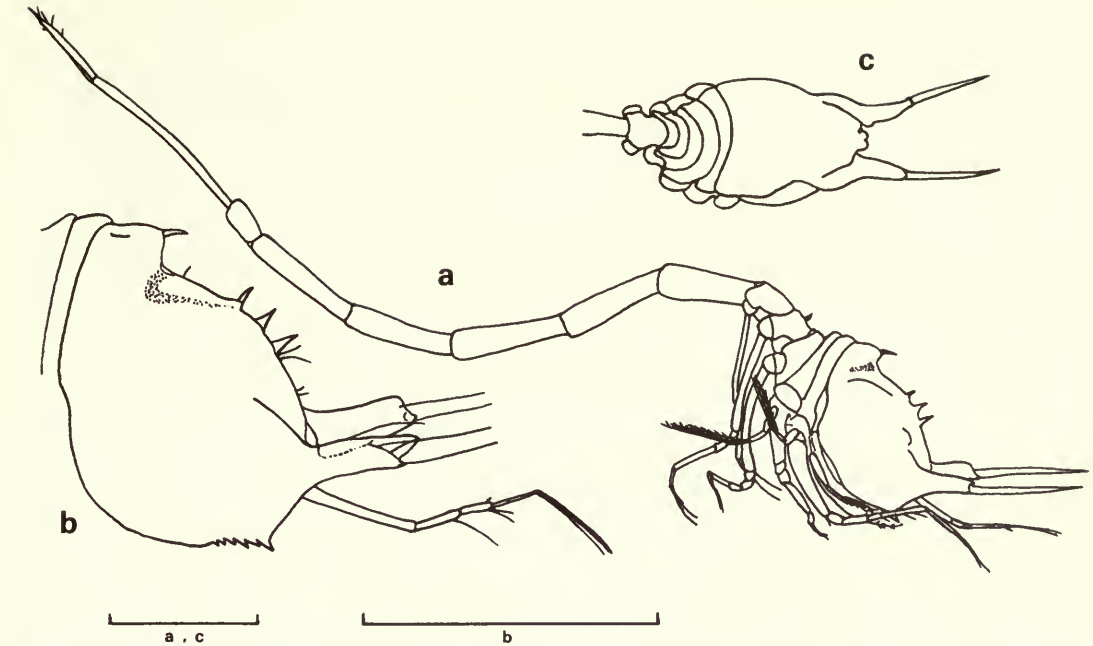

Fig. 7 *Cumella vemae* ♀, (a) lateral view; (b) carapace from side; (c) carapace and pereon from above.

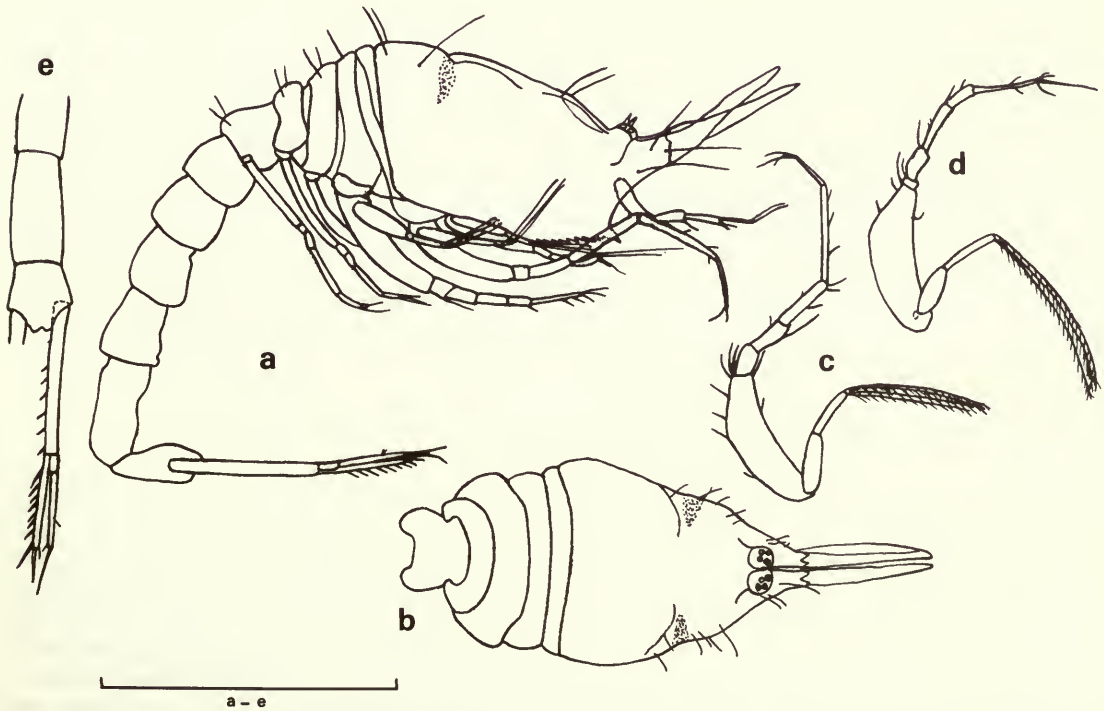

Fig. 8 *Cumella divisa* ♀, (a) lateral view; (b) carapace and pereon from above; (c) pereopod 1; (d) pereopod 2; (e) uropod and end of pleon.

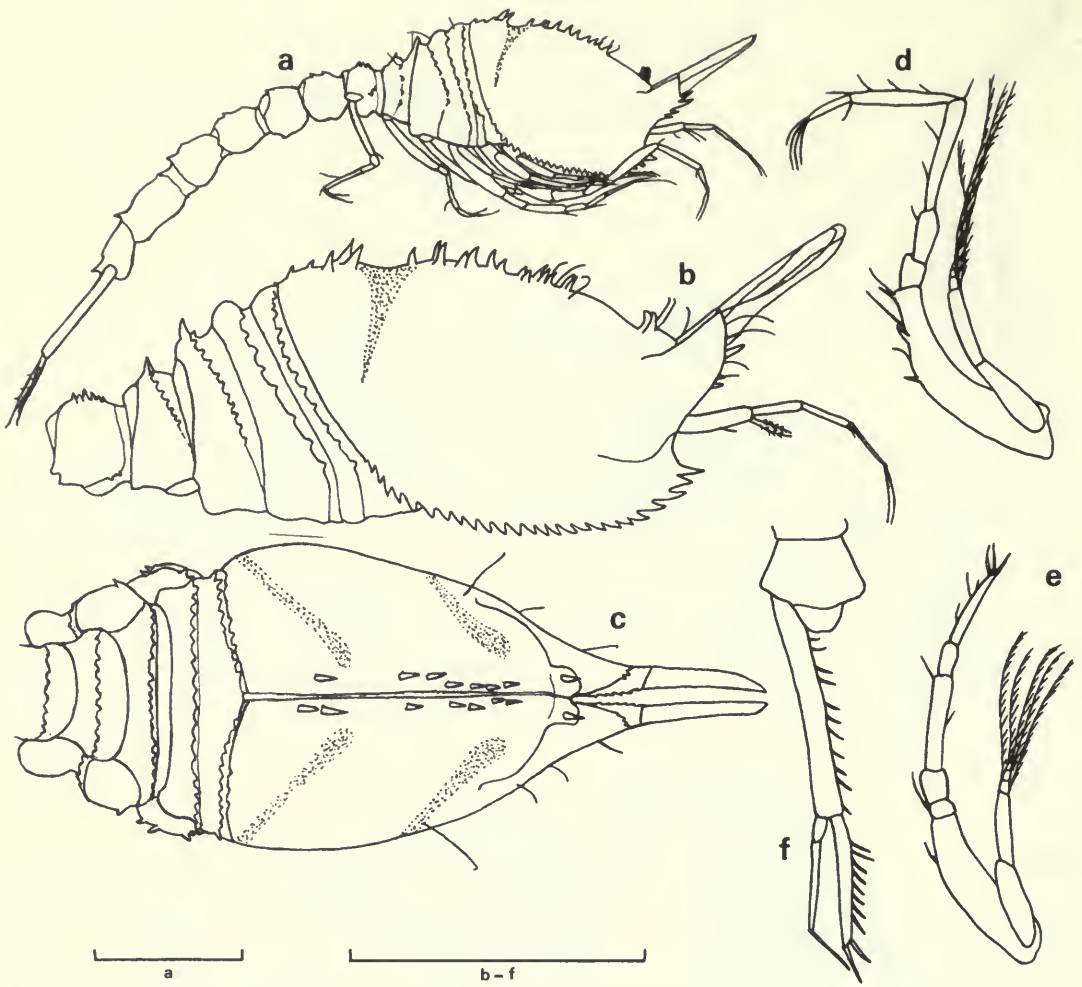

Fig. 9 *Cumella spinosa* ♀, (a) lateral view; (b) carapace and pereon from side; (c) carapace and pereon from above; (d) pereopod 1; (e) pereopod 2; (f) uropod and end of pleon.

DISTRIBUTION. Recorded from the NE. Atlantic, Biscay, off Dakar and SW. Africa from the upper slope downwards, 610 to 2864 m. depth.

Cumella spinosa sp. nov.
(Fig. 9)

MATERIAL. All 60-262: 2 ad. ♀♀, 3 imm. ♀♀.

DESCRIPTION. Adult female, length 4·4 mm: carapace (Fig. 9a–c) about $1\frac{3}{4}$ as long as high with pseudorostrum fairly short and upturned at about 30°. Siphons fairly long and a little separated. Dorsal outline a little convex, with an irregularly doubled row of fairly prominent teeth, about 8 on either side of the mid-dorsal line. The eyelobe is short and distinctly doubled, with a spine on each part. There are some forwardly directed spines about the antennal notch, which is well excavated. The antero-lateral angle is prominent and the lower edges of the carapace strongly serrated. Each pereonite carries a transverse row of spines, blunt on the side but more prominent mid-dorsally. There are a few spines on the pleon somites, of which the 6th is prominently produced between the bases of the uropods and rounded posteriorly.

Antenna 1 fairly long, with segments slender, the basal a little shorter than the second and third together, the second without a distal projection. Pereopod 1 (Fig. 9d) with the basis having a few prominent spines on its lower edge, about 2/3 as long as remaining segments together; carpus and propodus nearly equal in length and about twice as long as dactyl. Pereopod 2 (Fig. 9e) with basis about 2/3 as long as remainder of appendage; dactyl a little shorter than the carpus and twice as long as propodus. Pereopod 5 well developed. Uropod (Fig. 9f, g) of moderate length, with peduncle about as long as the last two pleon somites together, and with about 11 slender spines on its inner edge; it is about $1\frac{1}{2}$ as long as the endopod, which also carries a number of slender spines and is distinctly longer than the exopod.

TYPE LOCALITY. 36° 02.5′ S, 52° 17.9′ W, 2440–2480 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 294 : 1, paratypes 1982 : 295 : 4.

REMARKS. *C. spinosa* may be distinguished from *C. spinoculata* sp. nov. by the double spine row dorsally on the carapace. The pair of spines on the eyelobe is also curved backwards whereas it is forward pointing in the latter species.

DISTRIBUTION. 5 ♀♀ recorded at present from a single station in the Argentine basin.

Cumella spinoculata sp. nov.
(Fig. 10)

MATERIAL. SMBA-ES59: 3 imm. ♀♀. ES129: 1 imm. ♂, 1 ad. ♀. ES135: 1 imm. ♂. ES143: 1 juv. ES147: 1 imm. ♂, 2 ad. ♀♀. BIOGAS I-DS11: 2 imm. ♂♂. DS12: 2 ad. ♀♀. POLYGAS-DS15: 5 imm. ♂♂, 10 ad. ♀♀, 5 imm. ♀♀, 2 juv. DS17: 1 imm. ♀. DS18: 2 imm. ♂♂, 2 ad. ♀♀, 8 imm. ♀♀. BIOGAS III-DS35: 3 ad. ♀♀. DS36: 2 imm. ♂♂, 1 juv. BIOGAS IV-DS52: 1 imm. ♀, 1 juv. DS62: 1 imm. ♀. DS63: 1 imm. ♂. DS64: 1 min. ♂, 2 imm. ♀♀. BIOGAS VI-DS86: 1 imm. ♂. DS87: 1 imm. ♂, 2 imm. ♀♀. CP24: 1 imm. ♂, 1 ad. ♀. Ch106-313: 2 imm. ♂♂, 3 ad. ♀♀.

DESCRIPTION. Adult female, length 4·4 mm: carapace (Fig. 10a–c) nearly twice as long as high with pseudorostrum moderately long and upturned at about 25°; from the side it is acutely pointed at the upper edge. The siphons are separated and fairly long. The dorsal outline is convex but without spines except for a pair of prominent spines on the doubled eyelobe. There are some forwardly directed spines at the lower edge of the pseudorostrum. The antennal notch is well excavated and the antero-lateral angles marked by a long strong spine, behind which a series of strong serrations extends back on either side to the lower hind edge. There is a well marked depression on the dorsal part of the carapace about $\frac{3}{4}$ of its length towards the hind edge. A transverse row of blunt teeth is present on each of the pereon somites and some long scattered hairs occur on these and on the carapace. There are some fairly prominent teeth on the pereon epimera. The pleon is moderately long and each somite has a few blunt teeth laterally or ventrally, with a fairly prominent one mid-dorsally at the hind end of the 5th pleonite. The 6th somite is well produced between the bases of the uropods and rounded behind but ending in a single tooth.

Antenna 1 (Fig. 10d) is fairly long. The segments decrease successively in length and the basal segment has a distal spine. The pereopods (Fig. 10f, g) are generally similar to those of *C. spinosa* but a little more slender. The uropod peduncles (Fig. 10h) are considerably shorter than the last two pleonites together but these appendages differ little in other respects from those of *C. spinosa.*

TYPE LOCALITY. 47° 35.2′ N, 8° 40.1′ W, 2246 m. Type specimens deposited in the Museum National d'Histoire Naturelle, Paris. Holotype ♀ no. Cu 200, paratypes Cu 201.

REMARKS. This species is evidently closely related to *C. spinosa* and the most obvious distinguishing characters are noted under that species. It also seems close to *C. molossa* Zimmer from the Antarctic and may be identical with it. However, further specimens of *C. molossa* would be necessary to decide this and the differences in geographical range make it unlikely.

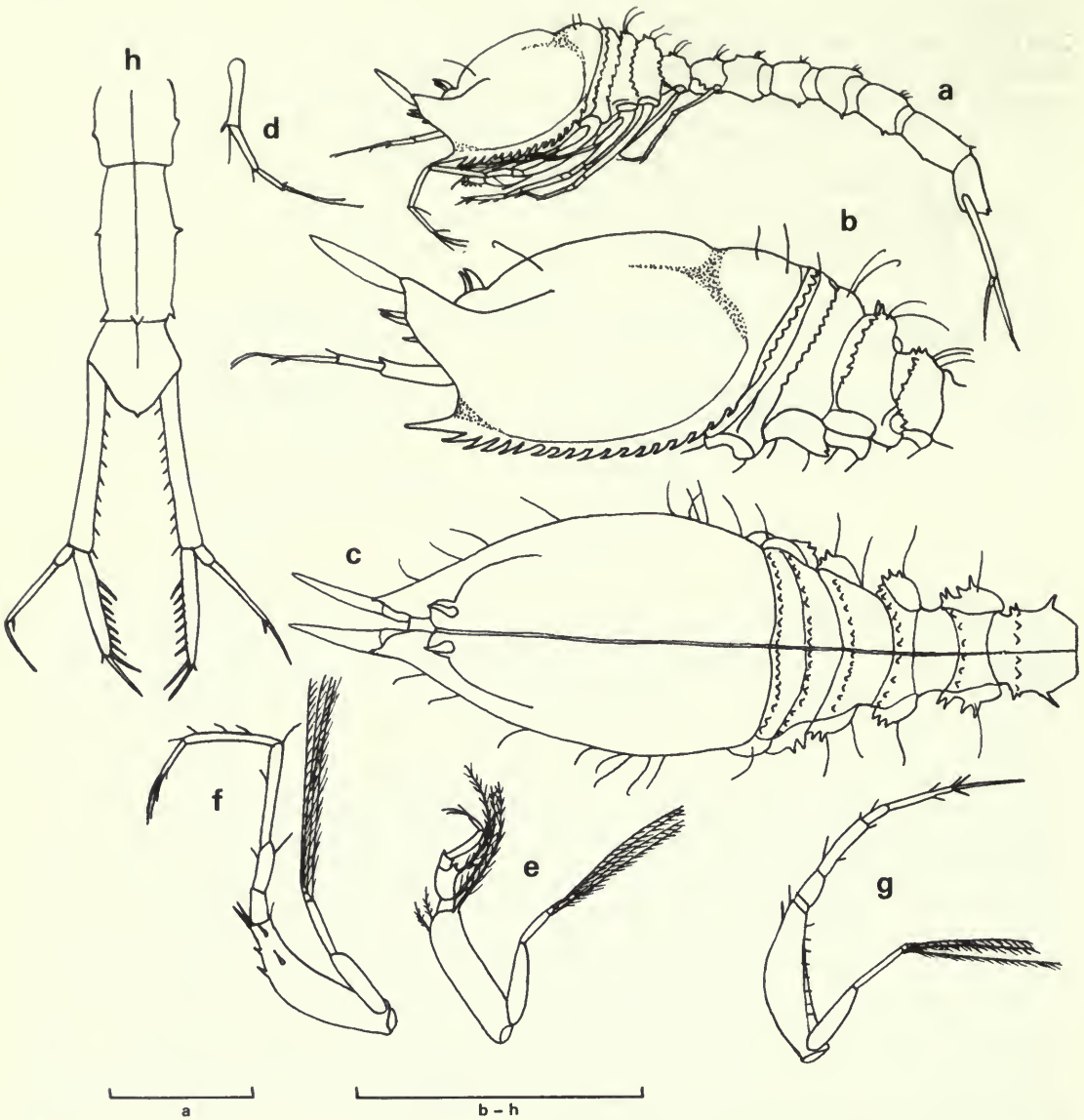

Fig. 10 *Cumella spinoculata* ♀, (a) lateral view; (b) carapace and pereon from side; (c) carapace and pereon from above; (d) antenna 1; (e) maxilliped 3; (f) pereopod 1; (g) pereopod 2; (h) uropods and end of pleon.

DISTRIBUTION. Collected at numerous stations in the Biscay area and from the west of Scotland between 1500 and 2900 m, from the lower slope downwards.

Cumella acuminata sp. nov.
(Fig. 11)

MATERIAL. POLYGAS-DS21: 6 ad. ♀♀, 2 juv. BIOGAS V-DS66: 3 ad. ♀♀. BIOGAS VI-DS86: 1 ad. ♀. AII31-142: 1 ad. ♂, 2 ad. ♀♀. 155: 3 imm. ♂♂, 6 ad. ♀♀, 3 imm. ♀♀. 156: 2 ad. ♂♂, 2 imm. ♂♂, 87 ad. ♀♀, 28 imm. ♀♀, 11 juv. 162: 1 imm. ♂, 1 ad. ♀, 1 imm. ♀. 167: 1 ad. ♂, 6 imm. ♂♂, 19 ad. ♀♀, 6 imm. ♀♀. Kn25-287: 1 imm. ♂, 6 ad. ♀♀, 3 imm. ♀♀. 291: 1 ad. ♀, 2 imm. ♀♀. 306: 2 imm. ♂♂, 7 ad. ♀♀, 9 imm. ♀♀, 1 juv. Ch106-321: 1 imm. ♀. 326: 1 imm. ♂ 1 imm. ♀. 328: 3 ad. ♀♀.

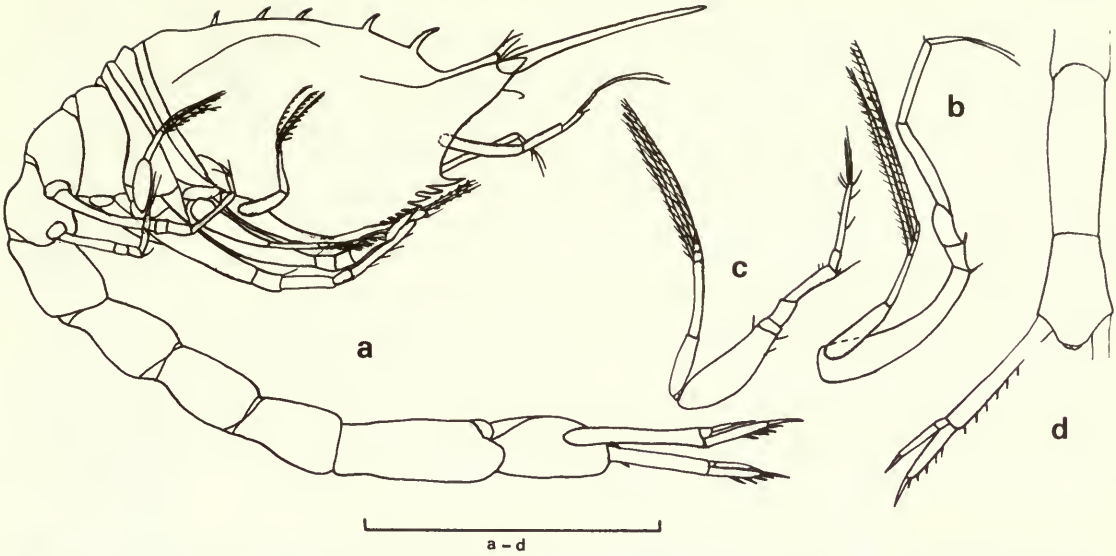

Fig. 11 *Cumella acuminata* ♀, (a) lateral view; (b) pereopod 1; (c) pereopod 2; (d) uropod and end of pleon.

DESCRIPTION. Adult female, length 4·2 m: carapace (Fig. 11a) about $1\frac{3}{4}$ as long as deep, with about 5 or fewer narrow forward-pointing mid-dorsal spines, scattered hairs in some individuals, sometimes hexagonal reticulation visible on its sides. The pseudorostrum is fairly long and only a little turned up from the line of the dorsum; siphons very long. The eyelobe is long and narrow, ending in a spine projecting beyond the pseudorostrum. The antennal notch is little excavated and there is a fairly large spine at the antero-lateral angle followed by a short row decreasing in size. Pereon unarmed or with a few short dorsal spines. Pleon unarmed or with a row of mid-dorsal spines and moderately long; pleonite 6 with a rounded backward projection.

Antenna 1 fairly long, with basal segment about twice as long as second, which is longer than the third. Perepod 1 (Fig. 11b) with basis narrow and unarmed, about $\frac{2}{3}$ as long as rest of appendage; the carpus is a little longer than the propodus which is more than twice as long as the dactyl. Pereopod 2 (Fig. 11c) with basis a little more than $\frac{2}{3}$ as long as more distal segments together; the dactyl is longer than the carpus and more than three times as long as the propodus. Uropods (Fig. 11d) with peduncle fairly short but not broadened, usually distinctly shorter than pleonite 5 and twice as long as the endopod, which is distinctly longer than the exopod; peduncle and endopod have some short spines on their inner edges.

TYPE LOCALITY. 00° 46′ S–00° 46.5′ S, 29° 24′ W, 3459 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 296 : 1, paratypes 1982 : 297 : 12.

REMARKS. *C. acuminata* resembles in its general aspect *C. meridionalis* sp. nov. (Fig. 26) but may easily be distinguished by its much longer eyelobe.

DISTRIBUTION. Found from mid-slope out to abyssal depths, 943–5000 m, from the Biscay area and off Dakar, and from Surinam and off Recife.

Cumella aculeata sp. nov.
(Fig. 12)

MATERIAL. POLYGAS-DS21: 1 imm. ♀. DS22: 1 imm. ♀. DS23: 1 ad. ♂. DS28: 1 ad. ♂, 3 imm. ♀♀. BIOGAS III-DS48: 1 imm. ♂. BIOGAS IV-DS52: 2 imm. ♀♀. BIOGAS VI-DS78: 1 juv. DS79: 2 ad. ♂♂, 1 imm. ♂, 1 ad. ♀, 3 imm. ♀♀, 3 juv. CP23: 5 imm. ♂♂, 15 imm. ♀♀. 5 juv. CP24: 1 imm. ♀.

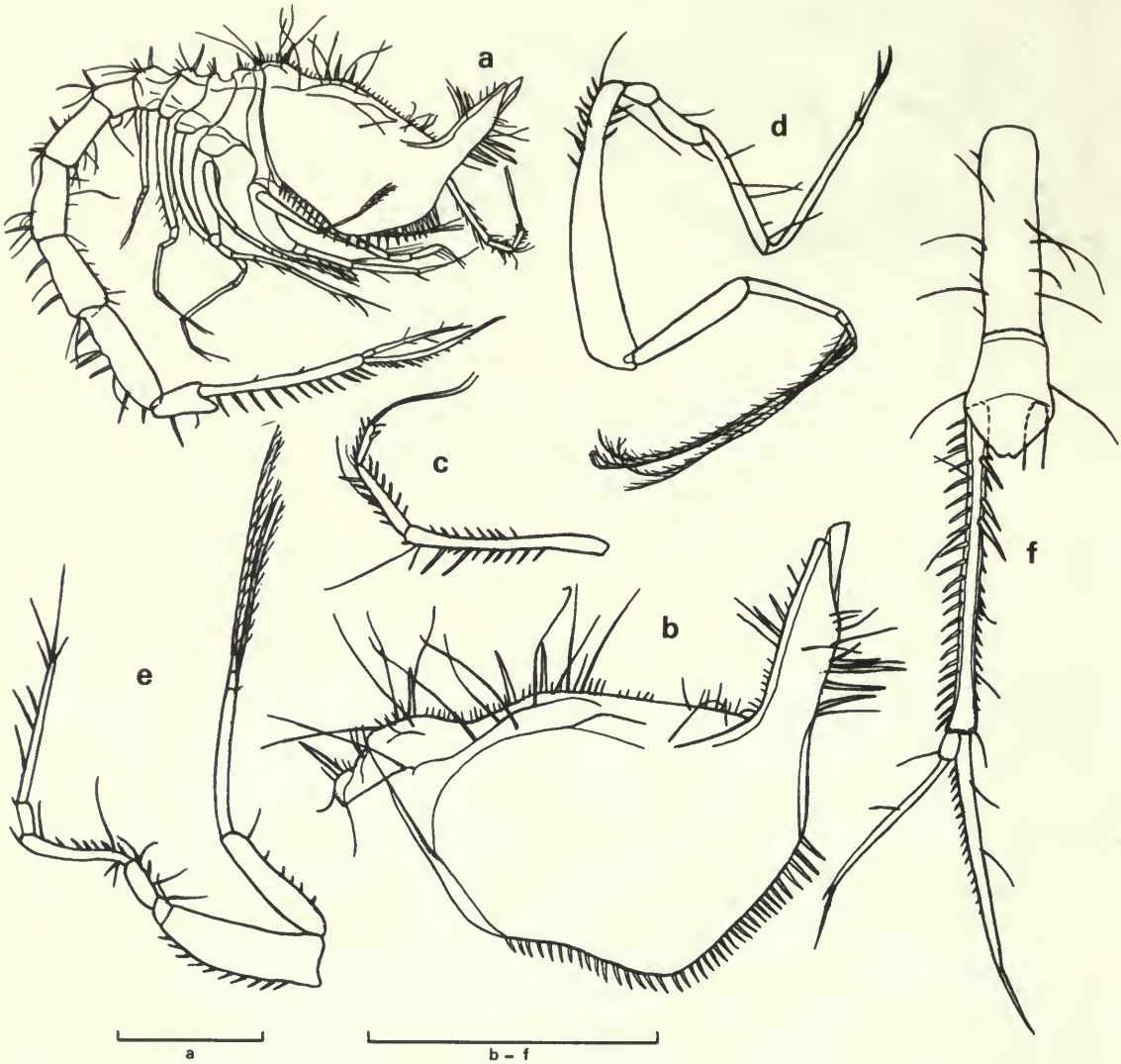

Fig. 12 *Cumella aculeata* ♀, (a) lateral view; (b) carapace from side; (c) antenna 1; (d) pereopod 1; (e) pereopod 2; (f) uropod and end of pleon.

AII31-155: 1 ad. ♀. 159: 1 ad. ♂, 1 imm. ♂, 3 ad. ♀♀. 167: 4 imm. ♂♂. 169: 4 imm. ♂♂, 3 ad. ♀♀, 1 imm. ♀. Kn25-288: 1 imm. ♂, 1 imm. ♀, 1 juv. 291: 1 ad. ♀, 2 imm. ♀♀. 293: 1 imm. ♀. 297: 1 imm. ♂, 1 ad. ♀. 299: 3 imm. ♂♂, 1 ad. ♀, 2 imm. ♀♀, 1 juv. 301: 3 imm. ♂♂, 12 ad. ♀♀, 3 imm. ♀♀, 2 juv. 303: 1 juv.

DESCRIPTION. Adult female, length 5·6 mm: carapace (Fig. 12a, b) about $1\frac{1}{2}$ as long as high, its hind end raised and with a long pseudorostrum upturned at nearly a right angle. Some long fragile spines are present mid-dorsally, in two rows at the hind end, and on the pseudorostrum, with many short and some long hair-like setae, but the spines are often broken short in preserved specimens. In some specimens the whole body is covered with short spines. The eyelobe is short and rounded. There is sometimes a row of fairly long and slender fragile spines extending postero-laterally from each antero-lateral angle. Pereon and pleon somites have some long spines and many hairs dorsally and the pleon is fairly long with a short triangular posterior projection.

Antenna 1 (Fig. 12c) very long, the basal segment much longer than the second and third together, the second about twice as long as the third, and all three carrying slender spines of which a few are longer than the remainder. Pereopod 1 (Fig. 12d) with basis armed distally with slender spines, about $\frac{2}{3}$ length of remaining segments together; the propodus distinctly longer than the carpus and more than three times as long as the dactyl. Pereopod 2 (Fig. 12e) with spines on the basis, merus and carpus, the basis less than half as long as remaining segments together; the dactyl is about as long as the carpus and propodus together and more than four times as long as the propodus. Pereopod 5 normally developed. Uropods (Fig. 12f) long, with the peduncle about as long as the last two pleonites together, with rows of long slender spines and some setae, less than $1\frac{1}{2}$ as long as the endopod, which is distinctly longer than the exopod.

Adult male, length 5·7 mm: generally similar to female but the pseudorostrum is proportionately shorter and the antero-lateral angle is broadly rounded and more prominent. The peduncle of antenna 2 has a dense brush of setae and the flagellum reaches only as far as the hind end of the pereon.

TYPE LOCALITY. 08° 12.4′ N, 55° 50.2′ W, 2487–2500 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 298 : 1, allotype 1982 : 299 : 1, paratypes 1982 : 300 : 3.

REMARKS. This and the following species are easily distinguished from others by their long and upstanding pseudorostrum, long spines dorsally on the carapace and pereon somites and a fairly long and slender pleon. It differs from *C. echinata* sp. nov. (Fig. 13) in several characters: the pseudorostrum is set at a somewhat greater angle with the carapace; the eyelobe is not elongated and there are a number of differences in the armature of the appendages. In the male the second antennal flagellum is shorter than in *C. echinata*.

DISTRIBUTION. Found off Recife and Surinam and in Biscay between 500 and 5000 m depth.

Cumella echinata sp. nov.
(Fig. 13)

MATERIAL. MBAUK-65: 3 ad. ♀♀, 1 imm. ♀. IOS-6696: 6 imm. ♂♂ 14 ad. ♀♀, 1 juv. 6697: 1 imm. ♂, 1 ad. ♀, 2 imm. ♀♀. 6701: 2 ad. ♂♂, 2 imm. ♂♂, 3 ad. ♀♀, 1 imm. ♀. SMBA-ES18: 1 imm. ♂. ES20: 1 ad. ♀. *Thalassa* 73-Z447: 1 imm. ♂. Z451: 1 imm. ♂, 1 juv. BIOGAS VI-DS86: 2 imm. ♂♂, 2 ad. ♀♀. Ch106-313: 7 imm. ♂♂, 9 ad. ♀♀, 8 imm. ♀♀, 6 juv.

DESCRIPTION. Adult female, length 4·6 mm: carapace (Fig. 13a, b) less than twice as long as high with long pseudorostrum upturned at about 70°. Siphon long. There is a mid-dorsal row of spines which are especially long at the front but some spines are scattered all over the carapace and pereon. There is a very long and fragile spine at the antero-lateral angle with a row of more slender spines behind. The eyelobe is very long and narrow, projecting beyond the pseudorostrum. There are four rows of fragile spines on the pleon which is long and fairly slender. Pleonite 6 has a rounded projection between the uropods.

Antenna 1 (Fig. 13b) is long and slender with basal segment nearly three times as long as second and third combined; second with a prominent prolongation at upper end. Pereopod 1 (Fig. 13c) with rows of slender spines on upper and lower edges, about half as long as rest of appendage; propodus narrow, somewhat longer than carpus and more than twice as long as dactyl. Pereopod 2 (Fig. 13d) with basis unarmed, about half as long as rest of appendage; carpus with a row of slender spines on upper edge, distinctly shorter than the dactyl and nearly four times as long as the propodus. Pereopod 5 of normal length. Uropods (Fig. 13e) long, peduncle somewhat shorter than last two pleonites together, with a row of serrations on its outer edge and a row of slender spines on its inner edge; it is more than $1\frac{1}{2}$ as long as the endopod which is only a little longer than the exopod.

The adult male differs from the female in the usual respects. The second antennal flagellum reaches to the end of the pleon.

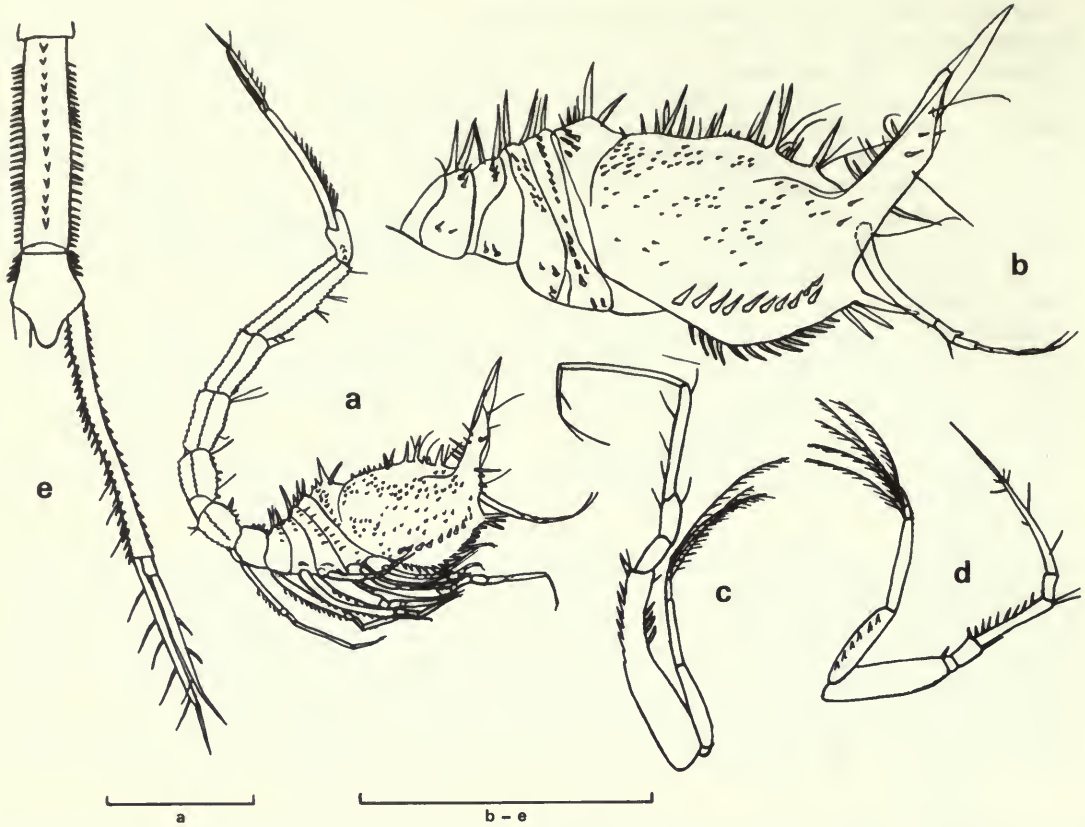

Fig. 13 *Cumella echinata* ♀, (a) lateral view; (b) carapace and pereon from side; (c) pereopod 1; (d) pereopod 2; (e) uropod and end of pleon.

TYPE LOCALITY. 51° 32.2′ N, 12° 35.9′ W, 1500–1491 m. Type species deposited in the British Museum (Natural History). Holotype 1982 : 301 : 1, allotype 1982 : 302 : 1, paratypes 1982 : 303 : 6.

REMARKS. Generally similar to *C. aculeata,* the more obvious differences have been noted below the description of that species.

DISTRIBUTION. Recorded from the NE. Atlantic, Biscay and Canary Islands from the lower slope, 1271–1950 m depth.

Cumella concinna sp. nov.
(Fig. 14)

MATERIAL. POLYGAS-DS15: 1 ad. ♂. DS16: 1 ad. ♂, 1 imm. ♂, 3 ad. ♀♀. BIOGAS III-DS36: 1 imm. ♂. DS37: 1 imm. ♀. BIOGAS IV-DS51: 2 ad. ♂♂, 2 imm. ♂♂, 1 ad. ♀, 2 imm. ♀♀.

DESCRIPTION. Ovigerous female, length 2·5 mm: carapace (Fig. 14a) fairly short, little more than 1½ as long as deep. Pseudorostrum very short, upturned, with fairly long siphons. Eyelobe short, not reaching end of pseudorostrum, its upper edge serrated. No mid-dorsal spines on carapace but minute serrations. Antero-lateral angle rounded with pointed spines below and serrations above. A transverse row of spines on pereon somites 3 and 4. Pleon somites not very slender with 3 longitudinal rows of short spines, a mid-dorsal and a ventro-lateral on either side. 6th pleonite not much produced posteriorly.

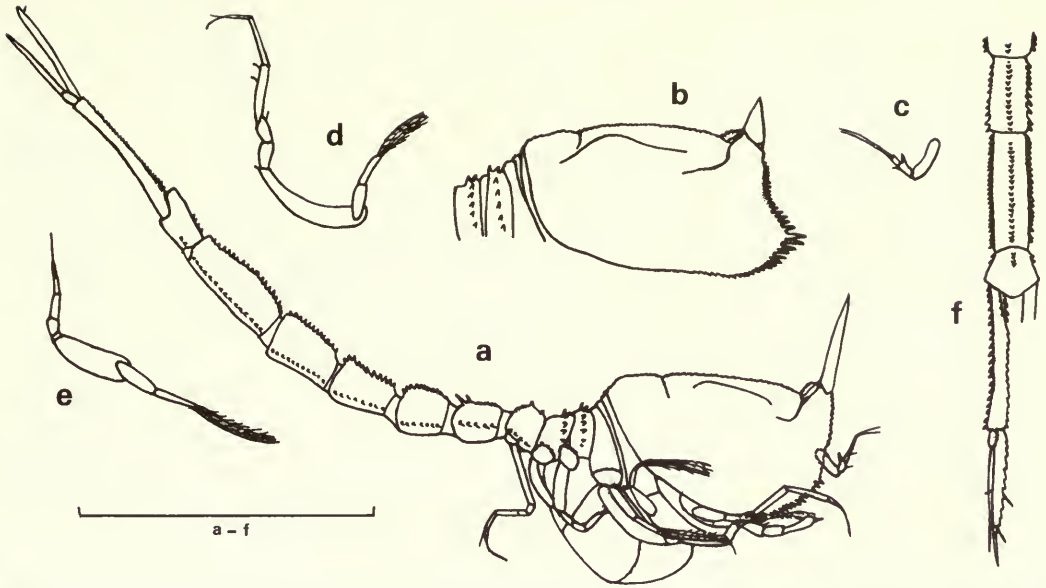

Fig. 14 *Cumella concinna,* (a) ovigerous ♀ from side; (b) adult ♂ carapace from side; (c) ♀ antenna 1; (d) pereopod 1; (e) pereopod 2; (f) ♀ uropod and end of pleon.

Antenna 1 (Fig. 14c) short; basal segment little more than twice as long as second, which has pronounced projection almost as long as third segment. Pereopod 1 (Fig. 14d) with basis more than half as long as remainder, carpus slightly longer than propodus and about twice as long as dactyl. Pereopod 2 (Fig. 14e) with basis about as long as other segments together, carpus longer than subequal propodus and dactyl. Pereopod 5 well developed. Uropod (Fig. 14f) moderately long with peduncle and inner edge of endopod serrated, the peduncle nearly three times as long as pleonite 6; endopod only a little longer than exopod, with few spines.

Adult male (Fig. 14b) with antero-lateral corner projecting well forward of pseudorostrum, with sharp spines above and below.

TYPE LOCALITY. 47° 36.1′ N, 8° 40.5′ W, 2325 m. Type specimens deposited in the Museum National d'Histoire Naturelle, Paris. Holotype ♀ no. Cu 202, allotype ♂ Cu 203, paratypes Cu 204.

REMARKS. *C. concinna* may be distinguished from other species in the genus by the combination of a short, sharply upturned pseudorostrum, carapace serrated mid-dorsally and at the front but without prominent spines, eyelobe rounded, not elongated, and serrated dorsally, and three rows of many short spines mid-dorsally and laterally on the pleon somites.

DISTRIBUTION. Found at present only in Biscay near the lower edges of the slope, 2110–2430 m.

Cumella exstans sp. nov
(Fig. 15)

MATERIAL. BIOGAS VI-DS74: 1 ad. ♀. DS76: 1 imm. ♀. DS79: 1 ad. ♂, 1 imm. ♂, 2 ad. ♀♀, 2 imm. ♀♀. CP09: 1 imm. ♀. AII31-142: 1 ad. ♂, 4 imm. ♂♂, 8 ad. ♀♀, 1 imm. ♀. 162: 1 ad. ♂, 1 imm. ♂, 2 ad. ♀♀. 169: 1 ad. ♂, 3 imm. ♂♂, 7 ad. ♀♀. AII42-202: 1 ad. ♀. Kn25-293: 3 ad. ♂♂, 6 ad. ♀♀.

DESCRIPTION. Adult ovigerous female, length 2·3 mm: carapace (Fig. 15a) shape generally similar to that of *C. erecta* but pseudorostrum much shorter; eyelobe a little elongated. No

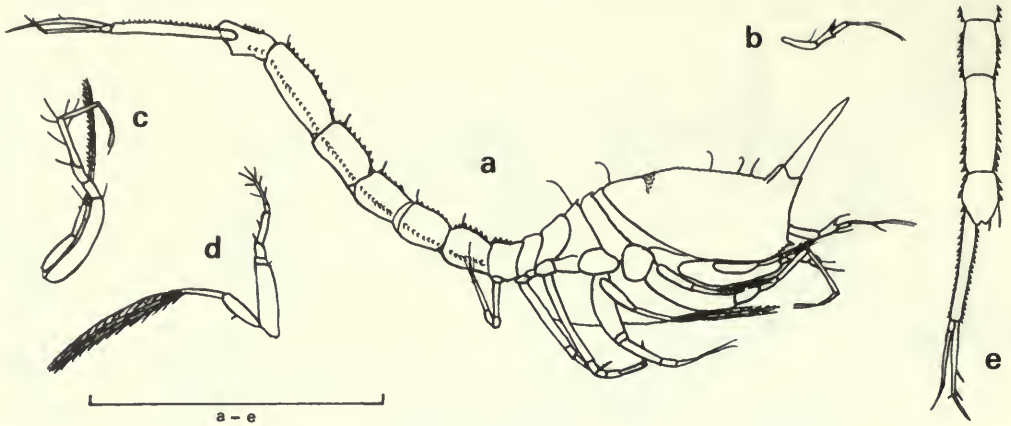

Fig. 15 *Cumella exstans* ovigerous ♀, (a) lateral view; (b) antenna 1; (c) pereopod 1; (d) pereopod 2; (e) uropod and end of pleon.

spines on carapace except small ones ventro-laterally but some setae. Pleon somites less slender than in *C. erecta* and with three longitudinal rows of hyaline serrations mid-dorsally and laterally; pleonite 6 not elevated posteriorly and moderately projecting between the uropods.

Antenna 1 (Fig. 15b) moderately long, with basal segment less than twice as long as second, which has a pronounced dorsal projection. Pereopod 1 (Fig. 15c) with basis slightly more than half as long as remaining segments together; carpus longer than propodus which is longer than dactyl. Pereopod 2 (Fig. 15d) with basis not much shorter than rest of appendage; carpus longer than dactyl. Pereopod 5 well developed and of normal length. Uropods (Fig. 15e) not very slender with peduncles serrated and about twice as long as pleonite 6 and 1½ as long as endopod.

TYPE LOCALITY. 8° 58′ N, 54° 04.3′ WE, 1456–1518 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 304 : 1, allotype 1982 : 305 : 1, paratypes 1982 : 306 : 4.

REMARKS. The combination of a short, sharply upturned pseudorostrum, carapace without spines but serrated dorsally, eyelobe a little elongated but not projecting beyond the tip of the pseudorostrum and three rows of many spines on the pleon somites distinguishes this species. It somewhat resembles *C. concinna* but differs in the shape of the eyelobe and the lack of a transverse row of spines on the posterior pereonites.

DISTRIBUTION. From mid-slope to abyssal plain on both sides of Atlantic from the tropics northwards to Biscay, 587 to 4715 m.

Cumella dayae sp. nov
(Fig. 16)

MATERIAL. AII42-201: 2 imm. ♀♀, 1 juv. 202: 1 imm. ♂, 4 juv. AII60-245: 8 imm. ♂♂, 26 ad. ♀♀, 15 imm. ♀♀.

DESCRIPTION. Adult female, length 3·7 mm: carapace (Fig. 16a, b) fairly short, little more than 1½ as long as high, slightly raised posteriorly, with about 8 mid-dorsal spines and a few hairs. The eyelobe reaches to the tip of the pseudorostrum which is not very long. Antero-lateral angle marked by a fairly prominent tooth, with a series of slight serrations behind. There are no spines on the pereon or the fairly slender pleon but pereonites 1 and 2 are produced dorsally. Pleonite 6 has a rounded backward projection between uropod peduncles.

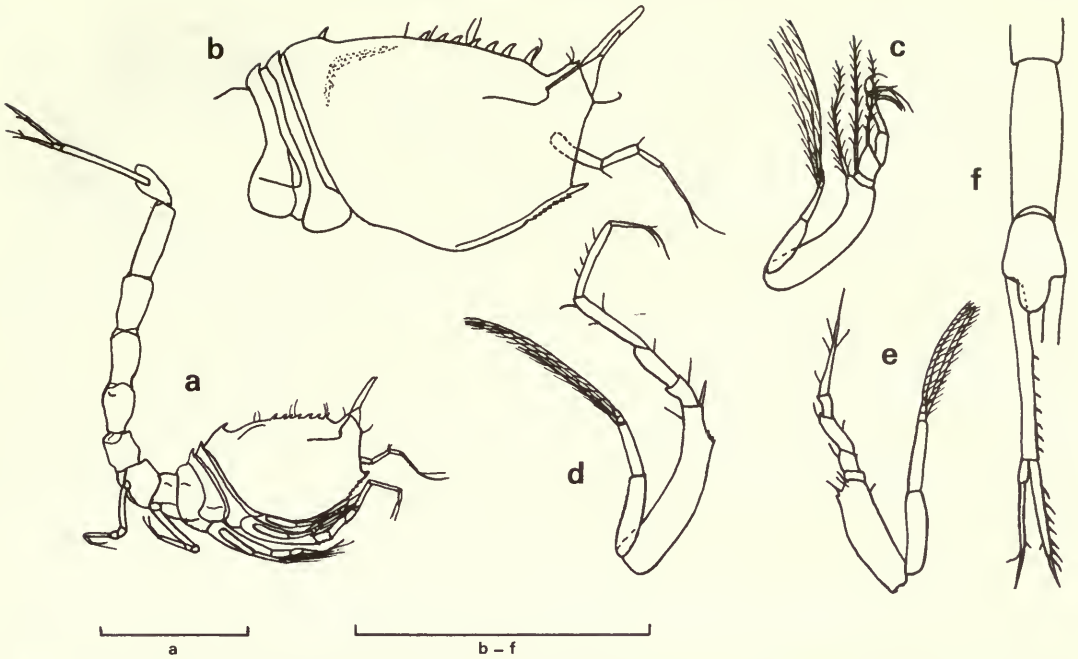

Fig. 16 *Cumella dayae* ♀, (a) lateral view; (b) carapace from side; (c) maxilliped 3; (d) pereopod 1; (e) pereopod 2; (f) uropod and end of pleon.

Antenna 1 (Fig. 16b) fairly long and slender, its basal segment a little shorter than the second and third together. Maxilliped 3 (Fig. 16c) with the basis slightly produced distally; merus broadened. Pereopod 1 (Fig. 16d) with basis with a few teeth on lower distal edge, not much more than half as long as remaining segments together; carpus and propodus subequal and each more than twice as long as dactyl. Pereopod 2 (Fig. 16e) with a few distal teeth on basis which is about $\frac{3}{4}$ length of remaining segments together, its dactyl a little longer than the carpus which is twice as long as the propodus. Pereopod 5 of normal length. Uropods (Fig. 16f) fairly slender, peduncles armed only with a series of short setae, distinctly shorter than pleonites 5 and 6 combined, barely twice as long as endopod, which is only a little longer than the exopod.

TYPE LOCALITY. 36° 55.7′ S, 53° 01.4′ W, 2707 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 307 : 1, paratypes 1982 : 308 : 8.

REMARKS. *C. dayae* has a short, fairly sharply upturned pseudorostrum, carapace with a single row of 8 mid-dorsal spines, eyelobe narrow and moderately elongated, and pleon unarmed.

DISTRIBUTION. Many off the Argentine coast and a few off SW. Africa, 1427–2707 m.

Cumella subducta sp. nov.
(Fig. 17)

MATERIAL. SMBA-ES12: 1 imm. ♂, 3 imm. ♀♀. ES14: 1 ad. ♀. ES18: 4 ad. ♂♂, 3 imm. ♂♂, 9 ad. ♀♀. ES20: 3 ad. ♂♂, 3 imm. ♂♂, 6 ad. ♀♀, 3 imm. ♀♀. ES22: 1 ad. ♂, 2 ad. ♀♀. BIOGAS I-DS13: 2 ad. ♀♀. POLYGAS-DS15: 1 ad. ♂, 3 imm. ♂♂, 6 ad. ♀♀, 1 imm. ♀. DS16: 1 imm. ♂, 2 ad. ♀♀. DS18: 2 ad. ♂♂, 1 imm. ♂, 8 ad. ♀♀. BIOGAS III-DS35: 2 imm. ♀♀. BIOGAS VI-DS86: 1 ad. ♀.

DESCRIPTION. Adult female, length 2·8 mm: carapace (Fig. 17a,b) fairly short, about $1\frac{1}{2}$ as long as deep, with a short pseudorostrum abruptly upturned at almost a rightangle. Siphons

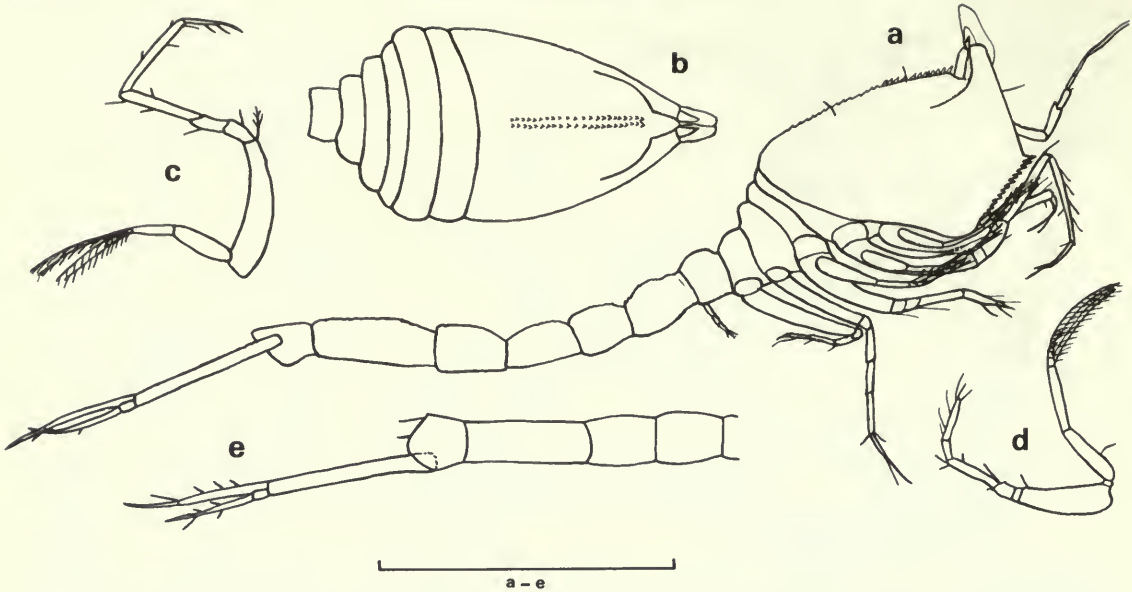

Fig. 17 *Cumella subducta* ♀, (a) lateral view; (b) carapace and pereon from above; (c) pereopod 1; (d) pereopod 2; (e) uropod and end of pleon.

short. There is a mid-dorsal double row of numerous short spines, the two rows set close together. The eyelobe is broad at the base and not very long, with a terminal spine. The antero-lateral angle is marked by a spine with a row behind it along the ventro-lateral border. Pereon and pleon are unarmed apart from a faint serration mid-dorsally along the pleon somites. Pleonite 6 triangular behind and little produced.

Antenna 1 (Fig. 17a) of moderate length with basal segment somewhat shorter than second and third combined, the second fairly stout with a short upper distal projection. Pereopod 1 (Fig. 17c) with basis half as long as remainder of appendage; propodus longer than carpus and more than twice as long as dactyl. Pereopod 2 (Fig. 17d) with basis about $\frac{3}{4}$ as long as remaining segments together; dactyl shorter than carpus but twice as long as propodus. Perepod 5 is normally very short and rudimentary but may be longer in some specimens. Uropod (Fig. 17c) of moderate length, basis with edges only faintly serrated, nearly as long as pereon somites 5 and 6 together and about twice as long as endopod, which is distinctly longer than the exopod.

TYPE LOCALITY. 47° 35.2′ N, 8° 40.1′ W, 2246 m. Type specimens deposited in the Museum National d'Histoire Naturelle, Paris. Holotype ♀ no. Cu 205, allotype ♂ Cu 206, paratypes Cu 207.

REMARKS. *C. subducta* resembles *C. dayae* in its general appearance but the pseudorostrum is more upturned from the horizontal, there is a double row of small spines on the dorsum of the carapace and the eyelobe is broad at the base with a terminal spine projecting beyond the tip of the pseudorostrum.

DISTRIBUTION. Many specimens obtained from the NE. Atlantic and Biscay on the lower slope and beyond, 1028–2325 m depth.

Cumella angustata sp. nov.
(Fig. 18)

MATERIAL. AII31-167: 7 imm. ♂♂, 10 ad. ♀♀, 2 juv.

DESCRIPTION. Adult female, length 3·5 mm: carapace (Fig. 18a,b) more than twice as long

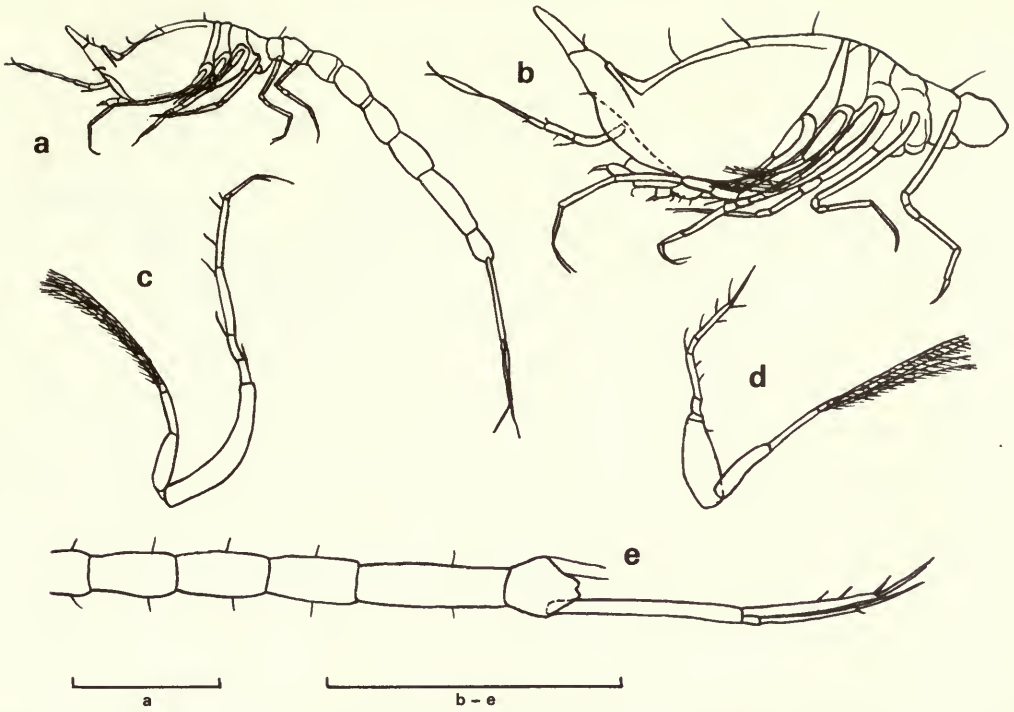

Fig. 18 *Cumella angustata* ♀, (a) lateral view; (b) carapace and pereon from side; (c) pereopod 1; (d) pereopod 2; (e) uropod and end of pleon.

as deep, unarmed except for a few long hairs dorsally. Pseudorostrum fairly long and upturned at about 45°. Siphons fairly long. Eyelobe long and narrow but much shorter than pseudorostrum. Antero-lateral border little excavated, with no antero-lateral angle nor serrations visible. Pereon and pleon somites unarmed, pleon long, with 6th somite produced backwards in triangular shape.

Antenna 1 (Fig. 18b) fairly long, with basal segment nearly twice as long as second, which in turn is nearly twice as long as third. Pereopod 1 (Fig. 18c) slender with basis curved, barely $\frac{2}{3}$ as long as remaining segments together; carpus and propodus about equal in length and each nearly twice as long as dactyl. Pereopod 2 (Fig. 18d) with basis broad, about $\frac{2}{3}$ as long as rest of appendage; carpus and dactyl about equal in length and each more than twice as long as propodus. Uropods (Fig. 18e) long and slender, with peduncles unarmed, somewhat shorter than pleonites 5 and 6 together and about $1\frac{1}{3}$ as long as the slender endopod, which is considerably longer than the exopod.

TYPE LOCALITY. 07° 58′ S–07° 50′ S, 34° 17′ W, 943–1007 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 309 : 1, paratypes 1982 : 310 : 3.

REMARKS. *C. angustata* has a fairly long pseudorostrum upturned at about 45° from the carapace which is unarmed apart from a few hairs, eyelobe narrow and elongated but much shorter than the pseudorostrum, pereon and pleon without spines or serrations.

DISTRIBUTION. Collected only from mid-slope off Recife, 943–1007 m depth.

Cumella erecta sp. nov.
(Fig. 19)

MATERIAL. MBAUK-65: 3 ad. ♀♀. IOS-6709: 1 ad. ♀. SMBA-ES10: 15 ad. ♂♂, 2 imm. ♂♂, 81 ad. ♀♀, 60 imm. ♀♀, 37 juv. ES12: 3 ad. ♂♂, 1 ad. ♀, 4 imm. ♀♀. ES15: 2 ad. ♂♂, 2 imm. ♂♂, 2 ad. ♀♀, 7 imm

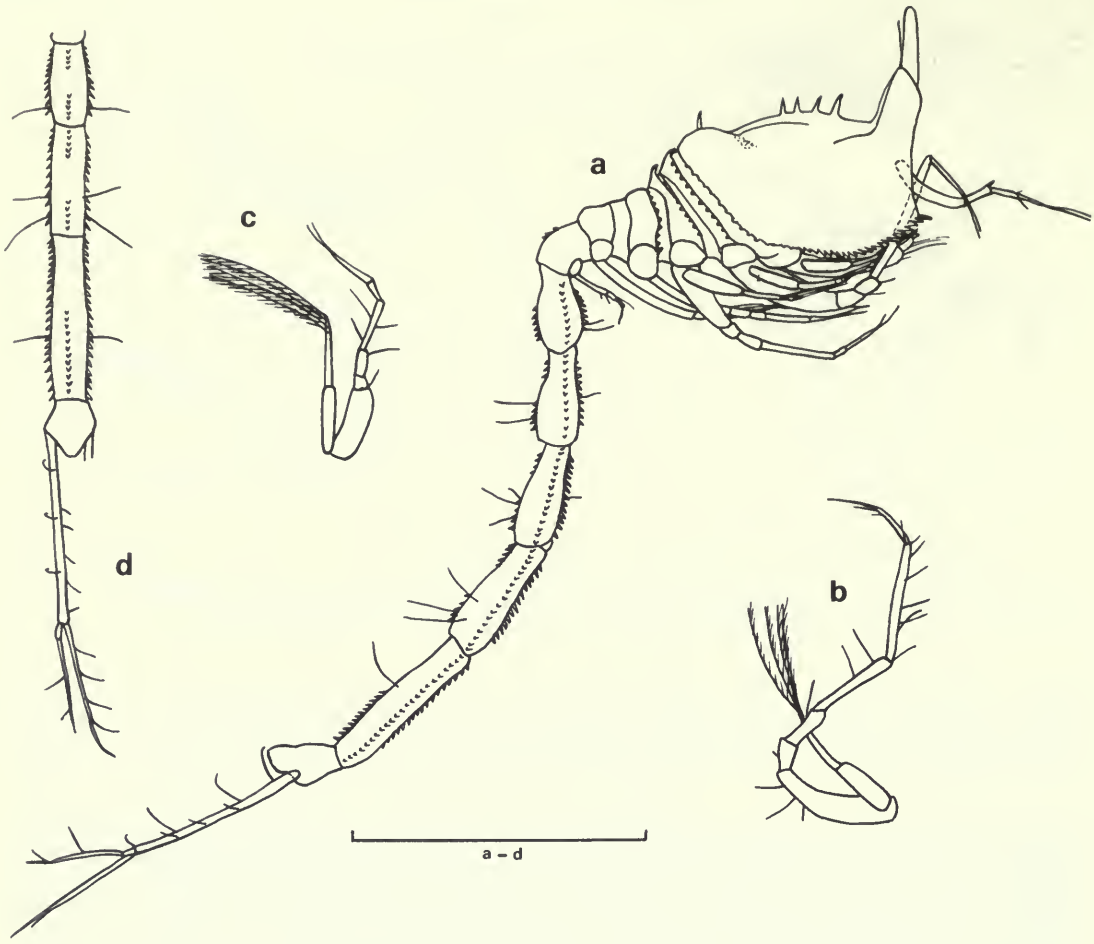

Fig. 19 *Cumella erecta* ♀, (a) lateral view; (b) pereopod 1; (c) pereopod 2; (d) uropod and end of pleon.

♀♀. POLYGAS-DS15: 5 ad. ♂♂, 4 imm. ♂♂, 25 ad. ♀♀, 2 imm. ♀♀. DS16: 1 ad. ♂. DS17: 1 imm. ♂, 3 imm. ♀♀. DS18: 1 imm. ♂, 2 ad. ♀♀. BIOGAS III-DS35: 1 imm. ♂. AII31-142: 1 ad. ♂, 5 imm. ♂♂, 3 ad. ♀♀, 1 imm, ♀, 1 juv. AII42-191: 1 imm. ♀. 202: 1 imm. ♀. Ch106–313: 1 ad. ♀, 2 juv.

DESCRIPTION. Adult female with empty marsupium, length 3·4 mm: carapace (Fig. 19a) similar in shape to that of *C. egregia* Hansen (Fig. 5) but with fewer dorsal spines and with shorter siphons. The pseudorostrum is fairly long and bent upwards at nearly a right angle to the dorsum of the carapace. The eyelobe is narrow and elongated to the tip of the pseudorostrum. There may be some long setae on the carapace and pleon somites. The latter are slender and have four longitudinal rows of short hyaline spines which are sometimes difficult to see. The 6th pleonite is raised and protrudes backwards between the uropods.

Antenna 1 (Fig. 19a) long and slender with the basal segment three times as long as the second, which has a pronounced projection as its upper distal end. Pereopod 1 (Fig. 19b) with the basis slender and little more than one third as long as the remaining segments together; the propodus is longer than the carpus and twice as long as the dactyl which ends in a slender curved spine. Pereopod 2 (Fig. 19c) with the more distal segments together about two and a half times as long as the basis; the dactyl is longer than the carpus and about four times as long as the propodus. Pereopod 5 is reduced in size and almost rudimentary.

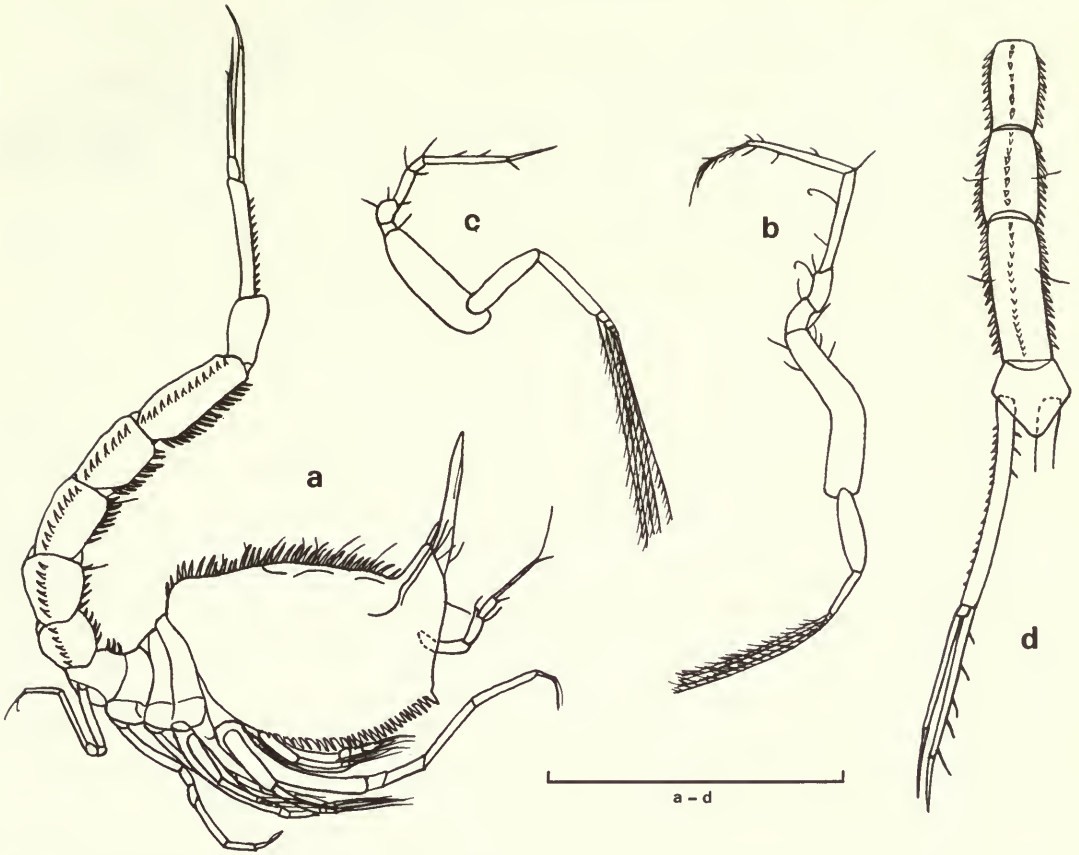

Fig. 20 *Cumella formosa* ♀, (a) lateral view; (b) pereopod 1; (c) pereopod 2; (d) uropod and end of pleon.

Uropods (Fig. 19d) long and slender, with the peduncle three times as long as the 6th pleonite and about twice as long as the endopod. They are unarmed except for some slender spines.

Adult male with eyelobe shorter than in female and pseudorostrum less upturned.

TYPE LOCALITY. 47° 35.2′ N, 8° 40.1′ W, 2246 m. Type specimens deposited in the Museum National d'Histoire Naturelle, Paris. Holotype ♀ no. Cu 208, allotype ♂ Cu 209, paratypes Cu 210.

REMARKS. *C. erecta* is evidently closely related to *C. egregia* Hansen (Fig. 5) but differs in having fewer but more prominent mid-dorsal spines on the carapace, a more erect pseudorostrum and no spines on the peduncles of the uropods.

DISTRIBUTION. An inhabitant of the lower slope, recorded between 1500 and 2351 m along the eastern side of the Atlantic.

Cumella formosa sp. nov.
(Fig. 20)

MATERIAL. AII60-245: 1 imm. ♂, 6 ad. ♀♀, 2 imm. ♀♀.

DESCRIPTION. Adult female, length 3·0 mm: carapace (Fig. 20a) not much more than 1½ as long as deep. Pseudorostrum fairly short, upturned at more than 45°. Eyelobe fairly long, reaching to end of pseudorostrum. A double row of numerous fairly long spines mid-dorsally

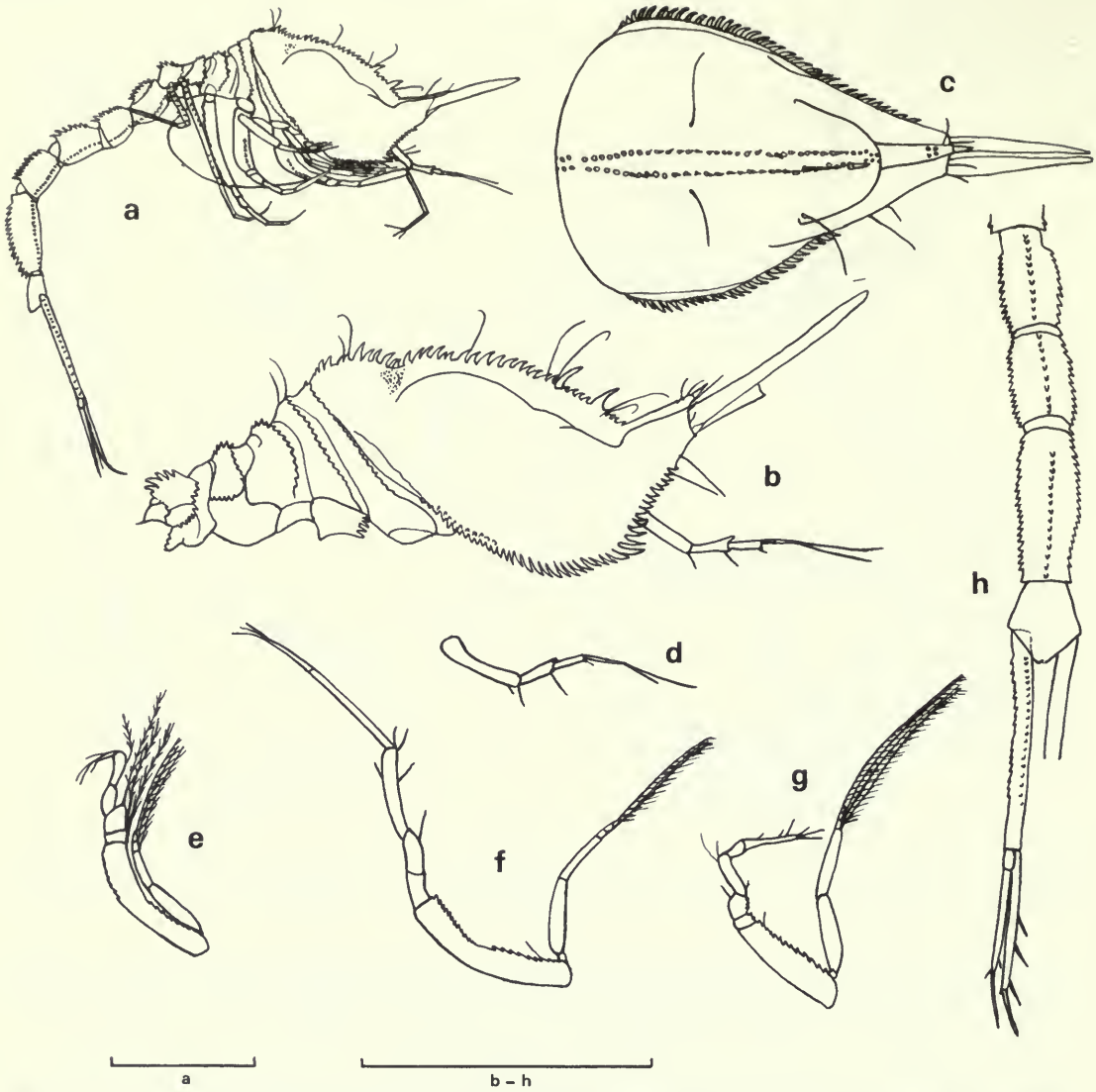

Fig. 21 *Cumella bishopi* ovigerous ♀, (a) lateral view; (b) carapace and pereon from side; (c) carapace from above; (d) antenna 1; (e) maxilliped 3; (f) pereopod 1; (g) pereopod 2; (h) uropod and end of pleon.

on carapace, and some hairs. Antero-lateral angle marked by a prominent spine with a row of sharp spines below and behind it. Pleon somites fairly stout, with mid-dorsal and ventro-lateral rows of fairly long spines. Pleonite 6 with triangular backward projection.

Antenna 1 (Fig. 20a) fairly long, with proximal segment about as long as second and third together, second rather broad with short distal projection, a little longer than third segment. Pereopod 1 (Fig. 20b) with basis a little more than half as long as remaining segments combined, its carpus and propodus equal in length and each more than twice as long as the dactyl. Pereopod 2 (Fig. 20c) with basis two thirds as long as remaining segments together, its dactyl twice as long as the carpus and five times as long as the propodus. Pereopod 5 normally developed. The uropods (Fig. 20d) fairly long, the peduncle serrated on the outer side and nearly as long as the last two pleonites together, the endopod somewhat shorter but distinctly longer than the exopod.

TYPE LOCALITY. 36° 55.7′ S, 53° 01.4′ W, 2707 m. Type specimens deposited in the British Musuem (Natural History). Holotype 1982 : 311 : 1, paratypes 1982 : 312 : 3.

REMARKS. Of the species of *Cumella* with a long narrow eyelobe, the pseudorostrum strongly upturned and with rows of spines on the pleon somites, only *C. formosa, C. bishopi* sp. nov. (Fig. 21) and *C. antipai* (Bacescu & Muradian) (Fig. 6) have a double row of spines mid-dorsally on the carapace. *C. formosa* differs from *C. antipai* in its shorter pseudorostrum and siphon, lack of lateral spines on the carapace and of a mid-ventral spine row on the pleon somites. From *C. bishopi* it differs in the shape of the carapace and lack of lateral spine rows on the pereon.

DISTRIBUTION. 9 specimens were collected from 2707 m off the Argentine coast.

Cumella bishopi sp. nov
(Fig. 21)

MATERIAL. Kn25-293: 2 ad. ♂♂, 24 imm. ♂♂, 51 ad. ♀♀, 23 imm. ♀♀.

DESCRIPTION. Ovigerous female, length 4·2 mm: carapace (Fig. 21a–c) fairly long, twice as long as high, with a moderately long pseudorostrum upturned at about 35° from the dorsum. Siphon long. A double row of numerous hooked spines with a few longer spines at the front extends back from the base of the eyelobe to the rear of the carapace. There is a row of hooked spines on either side starting above the antero-lateral angle and extending back postero-laterally. The eyelobe is as long as the pseudorostrum with a stout spine projecting forwards beyond it. The carapace has a few long hairs. Transverse rows of spines are present on the pereon and the moderately long pleon has three longitudinal rows. Pleonite 6 is triangular behind and not much produced.

Antenna 1 (Fig. 21d) is fairly long, the basal segment about as long as the second and third together, the second longer than the third and with a short distal projection. The basis of maxilliped 3 (Fig. 21e) is serrated basally above and distally below, without any distal projection, and the merus is fairly broad. Pereopod 1 (Fig. 21f) has a row of spines above on the basis which is a little more than half as long as the rest of the appendage; the propodus is distinctly longer than the carpus and twice as long as the dactyl. Pereopod 2 (Fig. 21g) has a row of spines on the upper edge of the basis, ischium and merus; the basis is about $\frac{3}{4}$ as long as the remainder of the appendage; the dactyl is longer than the carpus and more than twice as long as the propodus. Pereopod 5 is not particularly short. The uropod (Fig. 21h) is fairly long, with two rows of short spines on its peduncle, which is nearly as long as the last two pleonites together and about $1\frac{1}{2}$ times as long as the endopod, this being distinctly longer than the exopod.

The adult male has no spines dorsally and the antero-lateral angle is not specially prominent but rounded and produced.

TYPE LOCALITY. 8° 58′ N, 54° 04.3′ W, 1456–1518 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 313 : 1, allotype 1982 : 314 : 1, paratypes 1982 : 315 : 10.

REMARKS. *C. bishopi* resembles *C. formosa* in having a double row of spines mid-dorsally on the female carapace but the pseudorostrum is upturned at a smaller angle to the dorsal line of the carapace, which is longer and less deep in proportion. Some of the mid-dorsal spines towards the front of the carapace are more robust than the remainder and a further difference is the extension of the ventro-lateral row of spines on either side above the antero-lateral angle.

DISTRIBUTION. Recorded from Surinam from the lower slope at 1500 m depth.

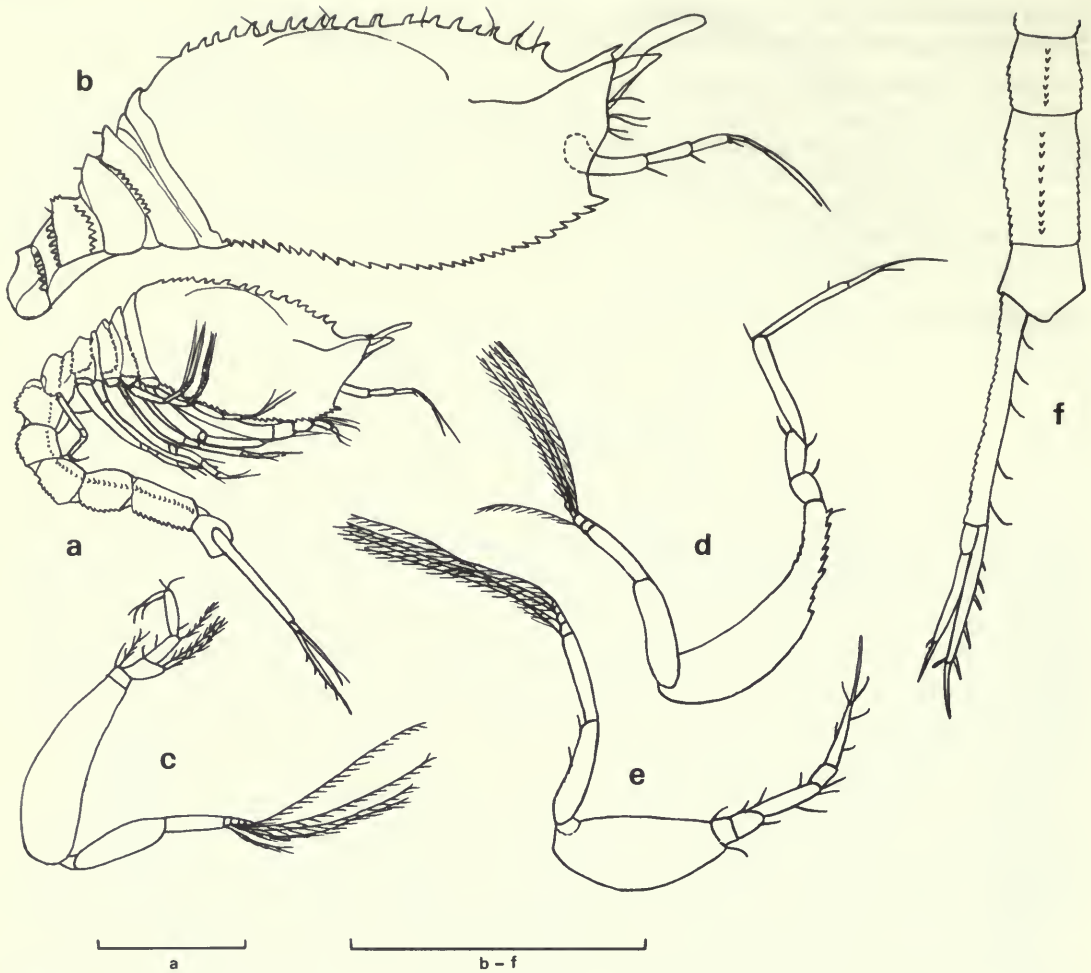

Fig. 22 *Cumella cristata* ♀, (a) lateral view; (b) carapace and pereon from side; (c) maxilliped 3; (d) pereopod 1; (e) pereopod 2; (f) uropod and end of pleon.

Cumella cristata sp. nov
(Fig. 22)

MATERIAL. POLYGAS-DS22: 2 ad. ♀♀. BIOGAS III-DS41: 3 imm. ♂♂, 4 ad. ♀♀.

DESCRIPTION. Adult female, length 4·3 mm: carapace (Fig. 22a, b) long, about twice as long as high, with a mid-dorsal crest of small teeth irregularly doubled extending from behind the eyelobe almost to the hind end. Pseudorostrum not very long, little upturned, and eyelobe reaching to its end with a spine projecting beyond it. Antero-lateral angle marked by a spine with a slight excavation above and a row of strong serrations below and behind. Pereon somites with lateral rows of short spines. Pleon somites fairly stout, serrated laterally and mid-dorsally. Pleonite 6 with short triangular projection posteriorly.

Antenna 1 (Fig. 22b) fairly long, with basal segment about as long as second and third together, the second a little longer than the third and without a distal projection. Maxilliped 3 (Fig. 22c) has no distal projection; the merus is broadened. Pereopod 1 (Fig. 22d) with basis serrated distally above and below, about $\frac{3}{4}$ as long as more distal segments together; the carpus and propodus about equal in length and each more than twice as long as the

dactyl. Pereopod 2 (Fig. 22e) with basis stout, a little shorter than remaining segments together; the dactyl a little shorter than the carpus and three times as long as the propodus. Pereopod 5 of normal length. Uropod (Fig. 22f) fairly long, with peduncle serrated on outer edge, and some fairly long setae on the inner edge, longer than last two pleonites together and much less than twice as long as the endopod, which is distinctly longer than the exopod.

TYPE LOCALITY. 47° 28.3′ N, 9° 07.2′ W, 3548 m. Type specimens deposited in the Museum National d'Histoire Naturelle, Paris. Holotype ♂ no. Cu 211, paratypes Cu. 212.

REMARKS. *C. cristata* and *C. longisipho* sp. nov. (Fig. 23) have the mid-dorsal spine row on the female carapace irregularly doubled but the pseudorostrum is not strongly upturned from the distal line of the carapace. In *C. cristata* the carapace is much more elongated than in *C. longisipho* and the pseudorostrum is not short, the eyelobe not projecting far beyond its tip.

DISTRIBUTION. An abyssal species, recorded from the Biscay area between 3548 and 4144 m depth.

Cumella longisipho sp. nov.
(Fig. 23)

MATERIAL. POLYGAS-DS20: 1 ad. ♂, 1 imm. ♂, 1 ad. ♀, 2 imm. ♀. BIOGAS IV-DS55: 2 imm. ♂♂, 3 ad. ♀♀, 1 imm. ♀, BIOGAS VI-DS78: 2 ad. ♀♀, 1 imm. ♀.

DESCRIPTION. Adult female, length 3·9 mm: carapace (Fig. 23a, b) little more than $1\frac{1}{2}$ as long as deep; dorsal outline irregular, with numerous broad hyaline spines set irregularly in two rows, and a few scattered hairs; the spines are often broken off. Pseudorostrum short, a little upturned. Siphons long. Eyelobe narrowed, longer than pseudorostrum. Antero-lateral angle marked by a hyaline spine followed by faint serrations. Pereon unarmed but first three somites somewhat raised dorsally. Pleon not very long, with a mid-dorsal and on either side a lateral row of faint hyaline serrations, sometimes scarcely visible. Pleonite 6 rounded posteriorly but little produced.

Antenna 1 (Fig. 23b) fairly long with basal segment nearly twice as long as second. Pereopod 1 (Fig. 23c) with basis about $\frac{3}{4}$ as long as rest of appendage; carpus distinctly longer than propodus and more than twice as long as dactyl. Pereopod 2 (Fig. 23d) with basis about $\frac{2}{3}$ as long as rest of appendage; carpus a little longer than dactyl and about three times as long as propodus. Uropods (Fig. 23e) fairly long, peduncle about as long as pleonites 5 and 6 together and $1\frac{1}{2}$ as long as the narrow endopod, which is distinctly longer than the exopod.

TYPE LOCALITY. 46° 31.2′ N, 10° 23.8′ W. 4706 m. Type specimens deposited in the Museum National d'Histoire Naturelle, Paris. Holotype ♀ no. Cu 213, allotype ♂ Cu 214, paratypes Cu 215.

REMARKS. *C. longisipho* has a short pseudorostrum with the eyelobe projecting well beyond it. The siphon is exceptionally long. There are fewer mid-dorsal spines on the carapace than in *C. cristata.*

DISTRIBUTION. Found at present only from the Biscay area in very deep water, from 4125–4706 m.

Cumella spicata sp. nov.
(Fig. 24)

MATERIAL. IOS-6701: imm. ♀.

DESCRIPTION. Immature female, length 3·7 m: carapace (Fig. 24a, b) twice as long as high with a single long forward-curving spine mid-dorsally behind the eyelobe and numerous long hairs. The pseudorostrum is long and acutely pointed and somewhat curved upwards. The siphons are not very long. The eyelobe is rudimentary and not at all elongated. The antennal

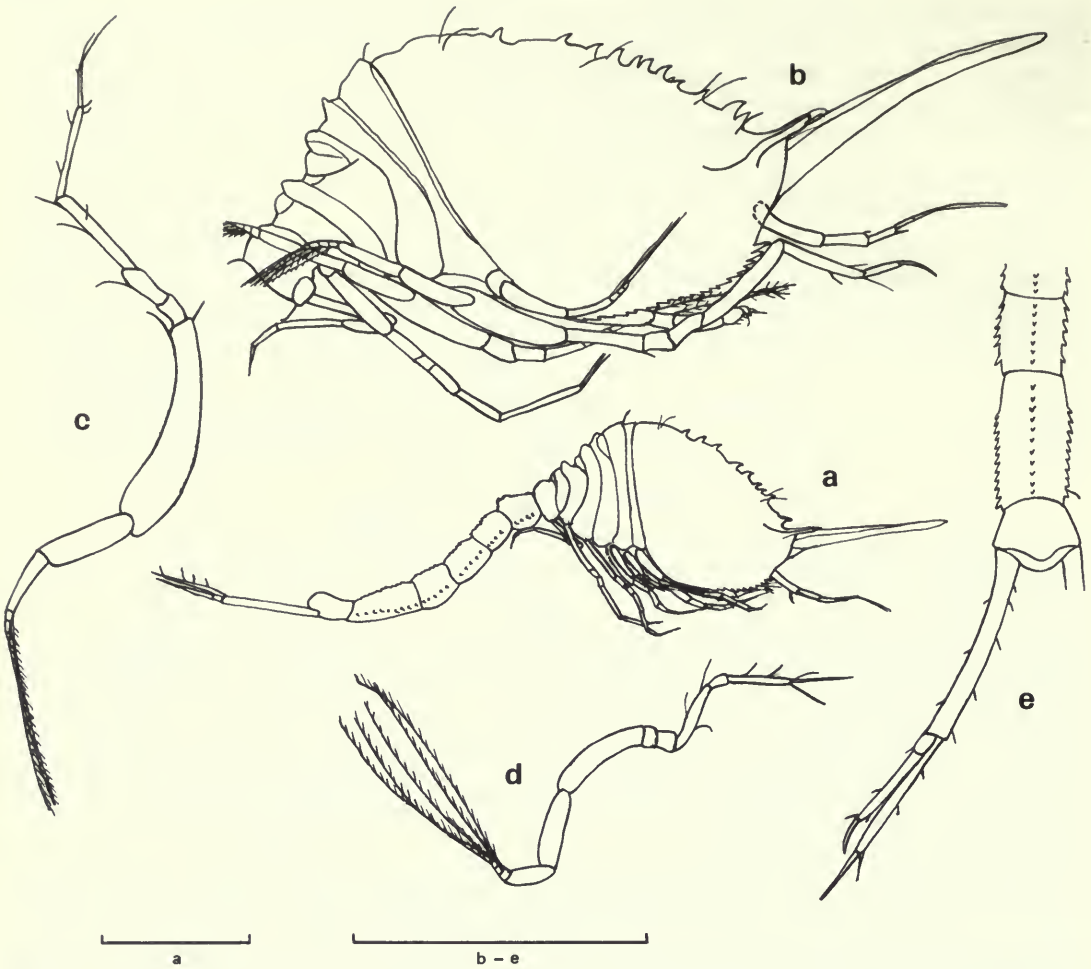

Fig. 23 *Cumella longisipho* ♀, (a) lateral view; (b) carapace and pereon from side; (c) pereopod 1; (d) pereopod 2; (e) uropod and end of pleon.

notch is excavated and the antero-lateral angle marked by a spine followed by a short row of serrations. There are a few strong spines dorsally on the pereon somites and these and the fairly long pleon have numerous hairs. The 6th pleonite is rounded behind and not much produced.

Antenna 1 with basal segment strongly curved, distinctly longer than the subequal second or third segments. Maxilliped 3 (Fig. 24c) with basis short and stout, little more than half as long as remaining segments together; ischium and merus broad; propodus longer than carpus and about twice as long as dactyl. Pereopod 1 (Fig. 24d) with basis about half as long as more distal segments together; carpus a little longer than propodus and about twice as long as dactyl. Pereopod 2 (Fig. 24e) with basis about as long as rest of appendage; the carpus is a little longer than the dactyl and about 1½ as long as the propodus. Uropods (Fig. 24f) comparatively short, the peduncle barely as long as pleonite 6 and less than 1½ as long as the endopod, which is distinctly longer than the exopod.

TYPE LOCALITY. 27° 45.2′ N, 14° 13′ W, 1934 m. The holotype deposited in the British Museum (Natural History). 1982 : 316 : 1.

REMARKS. Of the deep sea species of *Cumella* so far collected with the pseudorostrum

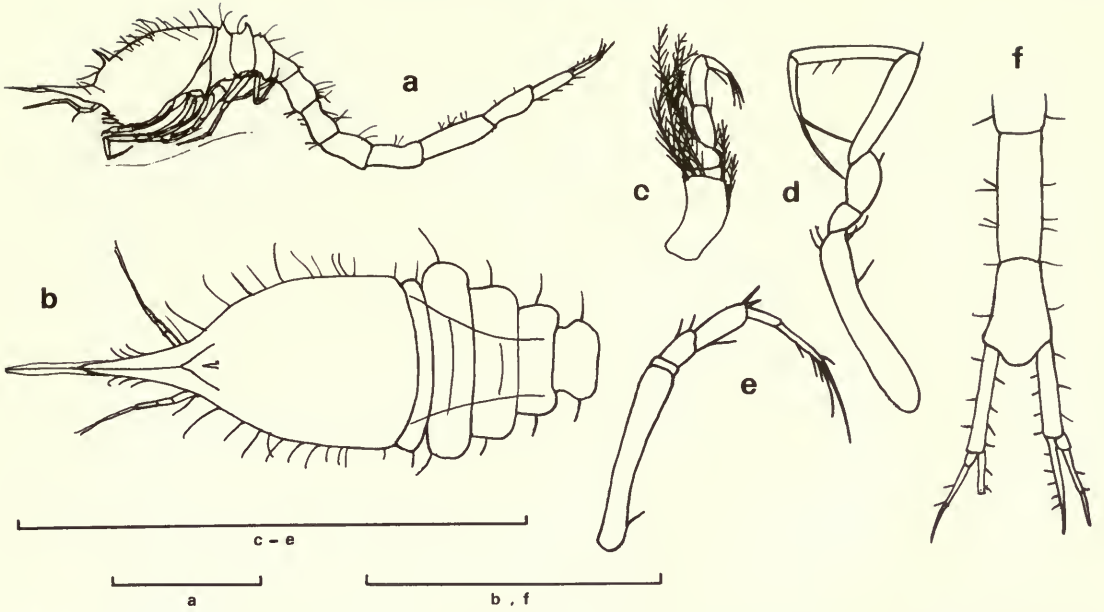

Fig. 24 *Cumella spicata* immature ♀, (a) lateral view; (b) carapace and pereon from above; (c) maxilliped 3; (d) pereopod 1; (e) pereopod 2; (f) uropods and end of pleon.

not strongly upturned and the eyelobe not doubled nor much elongated, *C. spicata* is distinguished by its long pointed pseudorostrum.

DISTRIBUTION. A single specimen collected from the edge of the slope off the Canary Isles in 1934 m depth.

Cumella polita sp. nov.
(Fig. 25)

MATERIAL. AII12-64: 1 ad. ♂, 1 imm. ♂, 4 ad. ♀♀. Ch50–76: 1 imm. ♂, 3 ad. ♀♀. Ch58–103: 1 ad. ♀. AII24-126: 1 ad. ♀. AII30-131: 1 imm. ♂, 1 ad. ♀, 1 imm. ♀.

DESCRIPTION. Adult female, length 4·0 mm: carapace (Fig. 25a, b) fairly well calcified with a shining appearance, less than twice as long as deep; the dorsal crest has four longish spines at the front followed by about 16 smaller spines. Pseudorostrum short and truncate, not upturned, and siphons very short. The eyelobe is oval but not elongated. Antennal notch distinctly excavated. The anterior pereon somites are raised dorsally but unarmed and the pleon is not very long. Pleonite 6 is rounded behind and hardly produced.

Antenna 1 (Fig. 25b) is fairly short with its basal segment only about as long as the second which has a dorsal projection distally. Maxilliped 3 (Fig. 25c) with basis a little longer than the remaining segments together, with a row of spines near its distal lower edge and the upper side produced distally; the merus is broadened and has a strong spine on its upper edge and another on the outer side; there are two spines on the upper edge of the carpus. Pereopod 1 (Fig. 25d) with basis about $\frac{3}{4}$ as long as rest of appendage; the carpus is a little longer than the propodus and twice as long as the dactyl. Pereopod 2 (Fig. 25e) has the basis also about $\frac{3}{4}$ as long remaining segments together; the dactyl is a little shorter than the carpus but twice as long as the propodus. Perepod 5 is normally developed. Uropod (Fig. 25f) fairly long, its peduncle distinctly shorter than the last two pleonites together and less than twice as long as the rather broad endopod, which is much longer than the exopod.

Adult male similar to female but without dorsal spines.

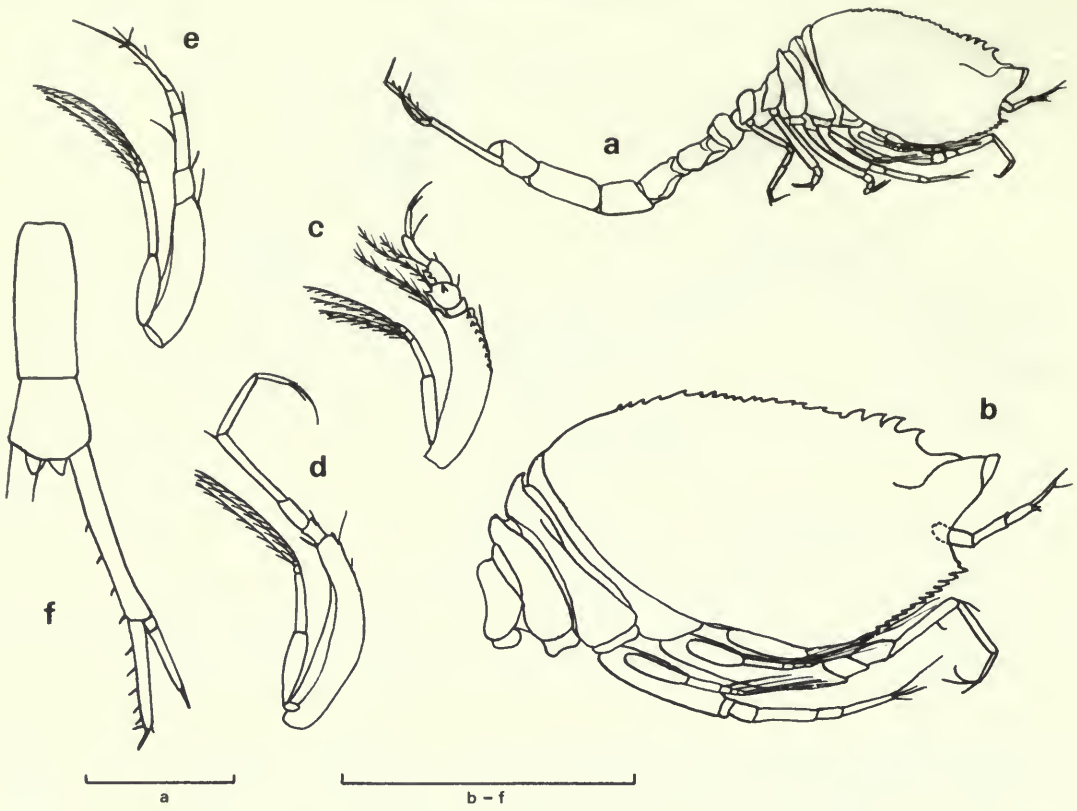

Fig. 25 *Cumella polita* ♀, (a) lateral view; (b) carapace and pereon from side; (c) maxilliped 3; (d) pereopod 1; (e) pereopod 2; (f) uropod and end of pleon.

TYPE LOCALITY. 38° 46′ N, 70° 06′ W, 2886 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 317 : 1, allotype 1982 : 318 : 1, paratypes 1982 : 319 : 2.

REMARKS. In *C. polita* the pseudorostrum is not at all upturned and the siphon is short; eyelobe is oval but not elongated, while in the female there are several large spines followed by about 16 smaller spines mid-dorsally on the carapace. The exopod peduncles are unserrated.

DISTRIBUTION. Recorded from the abyssal plain between Woods Hole and Bermuda between 2022 and 3806 m depth.

Cumella meridionalis sp. nov.
(Fig. 26)

MATERIAL. AII42-198: 1 imm. ♂, 1 imm. ♀. AII60-237: 1 juv. 239: 9 ad. ♂♂, 31 imm. ♂♂, 107 ad. ♀♀, 79 imm. ♀♀. 240: 8 ad. ♂♂, 3 imm. ♂♂, 47 ad. ♀♀, 27 imm. ♀♀, 8 juv. 243: 2 ad. ♀♀, 2 juv. 245: 1 imm. ♂, 6 ad. ♀♀, 2 juv. 246: 1 ad. ♂, 5 imm. ♂♂, 13 ad. ♀♀, 1 juv. 259: 6 imm. ♂♂, 23 ad. ♀♀, 5 imm. ♀♀. 262: 3 imm. ♂♂, 6 imm. ♀♀. 264: 5 ad. ♀♀, 5 juv. Kn25-299: 5 imm. ♂♂. 301: 16 imm. ♂♂, 7 ad. ♀♀, 3 juv. Ch106-328: 1 imm. ♀. 334: 1 juv.

DESCRIPTION. Ovigerous female, length 3·5 mm: carapace (Fig. 26a) nearly twice as long as high with usually five or fewer but up to 12 forward-pointing mid-dorsal spines and some short setae. The spines may be regularly spaced or occurring in groups. There is a low protuberance on either side of the frontal area. Pseudorostrum short, nearly horizontal,

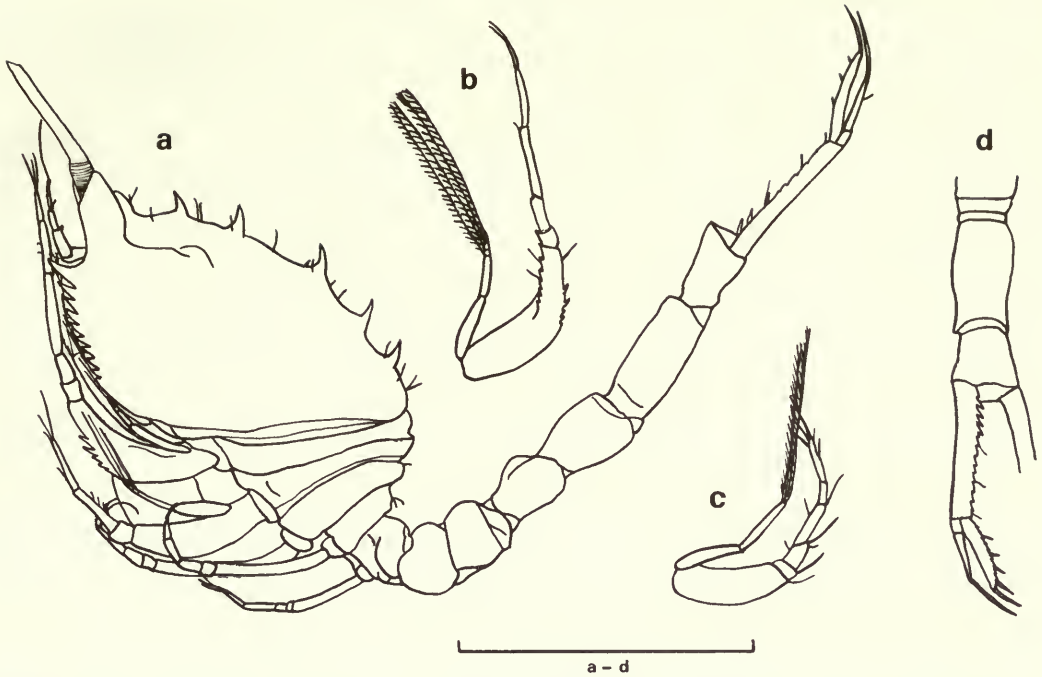

Fig. 26 *Cumella meridionalis* ovigerous ♀, (a) lateral view; (b) pereopod 1; (c) pereopod 2; (d) uropod and end of pleon.

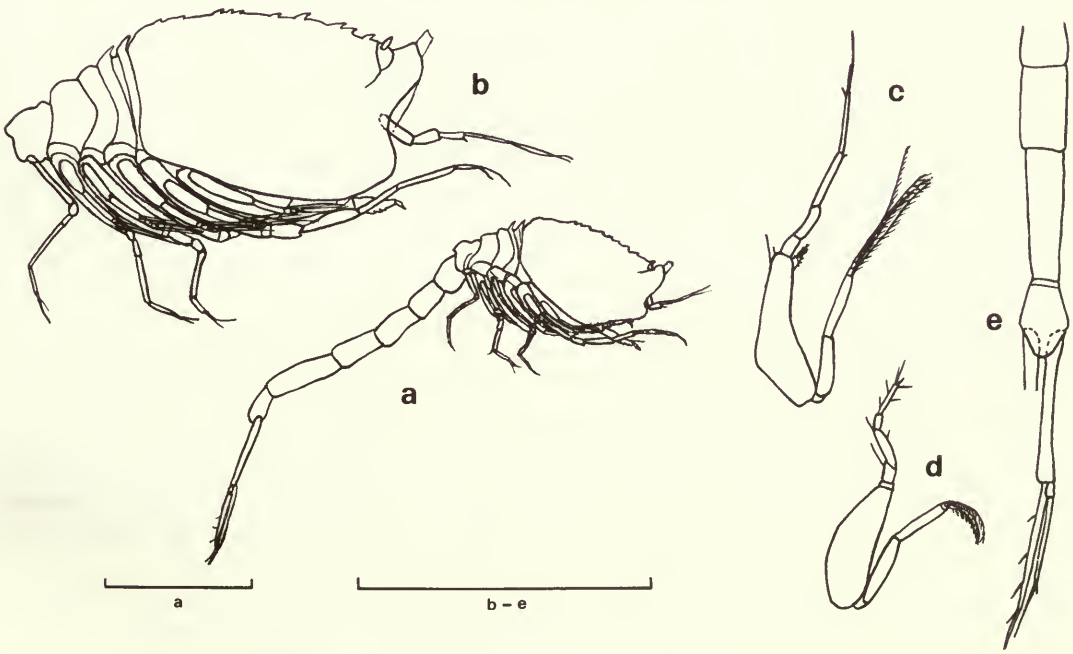

Fig. 27 *Cumella compacta* immature ♂, (a) lateral view; (b) carapace and pereon from side; (c) pereopod 1; (d) pereopod 2; (e) uropod and end of pleon.

siphons moderately long. Eyelobe not elongated. Antennal notch excavated and antero-lateral angle marked by a strong spine with a series behind it. Pereon and pleon somites are unarmed and the pleon is not much elongated, with pleonite 6 scarcely produced backwards.

Antenna 1 fairly short and stout with basal segment little longer than second. Pereopod 1 (Fig. 26b) with the basis strongly curved and with teeth on its upper and lower distal edges, about ¾ length of distal segments together; carpus somewhat longer than propodus, which is twice as long as dactyl. Pereopod 2 (Fig. 26c) with basis unarmed, about ¾ length of rest of appendage; carpus and dactyl about equal in length and each twice as long as propodus. Some adult females have reduced but not very rudimentary exopods on pereopods 3 and 4. Uropods (Fig. 26d) with peduncle fairly stout, much shorter than pleonites 5 and 6 together and almost twice as long as the fairly broad endopod, which is distinctly longer than the exopod; peduncle and endopod are both strongly serrated on their inner edges.

TYPE LOCALITY. 36° 49′ S, 53° 15.4′ W, 1661–1679 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 320 : 1, allotype 1982 : 321 : 1, paratypes 1982 : 322 : 12.

REMARKS. *C. meridionalis* has the pseudorostrum quite short and little upturned with the eyelobe not elongated and there are usually 5 but not more than 12 fairly large mid-dorsal spines on the carapace of the female and a low protuberance on either side of the frontal area. The uropod peduncles are strongly serrated on the inner edge.

DISTRIBUTION. Found from the mid-slope down to abyssal depths, from 993–4566 m from the NE. Atlantic and off Surinam, and from SW. Africa and Argentina in the South Atlantic.

Cumella compacta sp. nov.
(Fig. 27)

MATERIAL. AII31-162: 1 imm. ♂.

DESCRIPTION. Immature male, length 3·2 mm: carapace (Fig. 27a, b) about 1½ as long as deep with about 12 irregular broad mid-dorsal teeth. Pseudorostrum slightly upturned, short and truncate and siphons very short. Eyelobe fairly broad, not elongate, with one spine. Antero-lateral corner rounded and produced forwards, without teeth. Pereon and pleon unarmed, pleon fairly long, 6th pleonite fairly well produced behind.

Antenna 1 (Fig. 27b) of moderate length, basal segment distinctly longer than second which is fairly broad. Pereopod 1 (Fig. 27c) with basis about ¾ length of rest of appendage; carpus and propodus about equal in length and each twice as long as dactyl. Pereopod 2 (Fig. 27d) with basis slightly longer than rest of appendage; dactyl slightly shorter than carpus but twice as long as propodus. Pereopod 5 normally developed. Uropod (Fig. 27e) fairly long, peduncle not much longer than pleonite 5 or the endopod, which is narrow and much longer than the exopod.

TYPE MATERIAL. 08° 02′ S-07° 56′ S, 34° 03′ W-34° 09′ W, 1493 m. The holotype deposited in the British Museum (Natural History). 1982 : 323 : 1.

REMARKS. In *C. compacta* the pseudorostrum is short and scarcely upturned; the eyelobe is fairly broad, not elongated, with a single spine projecting from it and the carapace has a row of about 12 irregularly placed mid-dorsal spines; the antero-lateral angle is rounded and without spines or serrations. The uropods are slender with their peduncles unserrated.

DISTRIBUTION. A single specimen recorded from off Recife in 1493 m.

Cumella decipiens sp. nov.
(Fig. 28)

MATERIAL. SMBA-ES20: 2 imm. ♀♀. BIOGAS IV-DS52: 2 imm. ♀♀. BIOGAS VI-DS87: 1 ad. ♀.

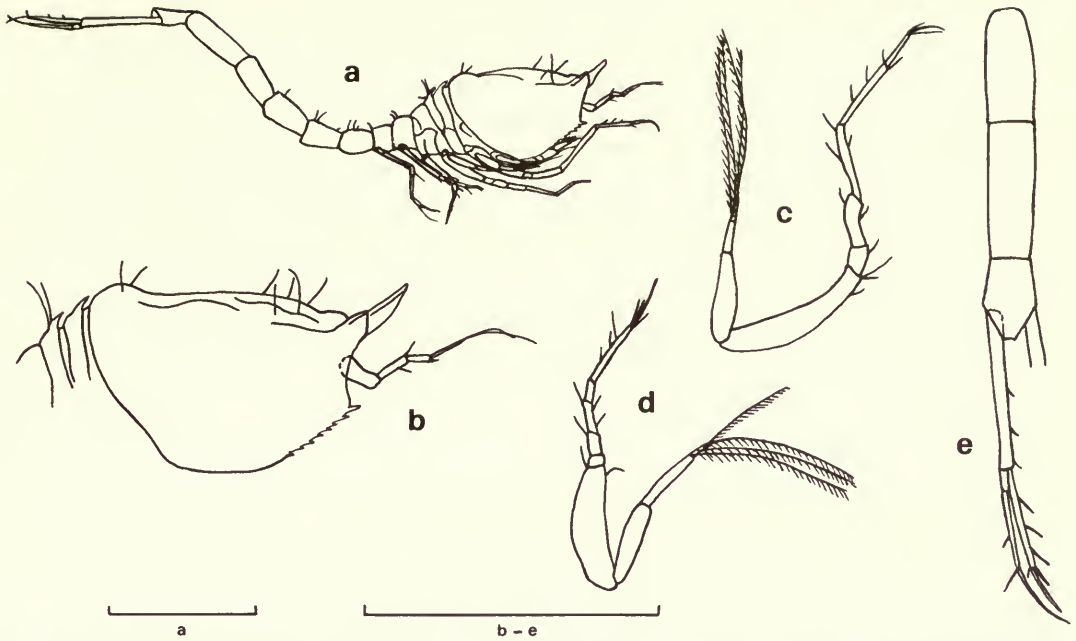

Fig. 28 *Cumella decipiens* ♀, (a) lateral view; (b) carapace from side: (c) pereopod 1; (d) pereopod 2; (e) uropod and end of pleon.

CP23: 4 ad. ♀♀. AII30-131: 2 ad. ♀♀. AII60-259: 2 ad. ♂♂, 8 ad. ♀♀, 7 imm. ♀♀. Kn25-293: 1 ad. ♂, 3 ad. ♀♀. 295: 8 imm. ♂♂, 4 ad. ♀♀, 2 juv. 297: 3 ad. ♀♀. 299: 1 ad. ♂, 6 imm. ♂♂, 4 ad. ♀♀.

DESCRIPTION. Adult female, length 3·3 mm: carapace (Fig. 28a, b) very similar in shape to that of *C. bishopi* but dorsal crest not usually apparent. There may be a few spines mid-dorsally but these are often broken off. The pseudorostrum is somewhat less truncate and the eyelobe is rounded and not elongated. The first two pereonites are raised dorsally. The pleon is unarmed except for scattered hairs and fairly long. The 6th pleon somite is well produced backwards and truncated.

Antenna 1 (Fig. 28b) not very long, with basal segment not much longer than second. Pereopod 1 (Fig. 28c) with basis more than half as long as rest of appendage; the carpus and propodus are about equal in length and each nearly twice as long as the dactyl. Pereopod 2 (Fig. 28d) with basis not much shorter than rest of appendage; the dactyl more than twice as long as the carpus and three times as long as the propodus. Pereopod 5 normally developed. Uropod (Fig. 28e) fairly long, its peduncle unarmed, much shorter than pleonites 5 and 6 together and about $1\frac{1}{2}$ as long as the endopod, which is very little longer than the exopod.

In the adult male the antero-lateral edges of the carapace are well produced forwards and rounded, with hyaline serrations, and the first antennal flagellum is long.

TYPE LOCALITY. 37° 13.3′ S, 52° 45′ W, 3305–3317 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 324 : 1, allotype 1982 : 325 : 1, paratypes 1982 : 326 : 4.

REMARKS. *C. decipiens* has the pseudorostrum short with a fairly short siphon and not much upturned; the eyelobe is rounded and not elongated and without a spine; the carapace has only a few mid-dorsal spines and these may be lacking; the antero-lateral angle has a fairly prominent spine in the female and a row of serrations behind.

DISTRIBUTION. Collected from the NW. and NE. Atlantic and Biscay and from off the Argentine and Surinam from mid-slope downwards in 500–3317 m depth.

Key to the Atlantic deep sea species of *Cumella*

1 Eyelobe doubled (Figs 7–10) 2
– Eyelobe single, rounded or elongate (Figs 4–6, 11–28) 5
2 Pseudorostral lobes and siphons widely separated; pleon long (Fig. 7) ***vemae*** (Bacescu, 1972)
– Pseudorostral lobes and siphons not widely separated (Figs 8–10) 3
3 Carapace with an irregularly double row of spines mid-dorsally (Fig. 9) ***spinosa*** sp. nov. (p. 218)
– Carapace without mid-dorsal spines (Figs 8, 10) 4
4 Pseudorostrum with some prominent forward-pointing spines below siphons (Fig. 10) ***spinoculata*** sp. nov. (p. 219)
– Pseudorostrum without forward-pointing spines (Fig. 8) ***divisa*** sp. nov. (p. 215)
5 Pseudorostrum upturned at an angle of 40° or more with the carapace (Figs 4–6, 12–20) 6
– Pseudorostrum set at an angle of 35° or less with the carapace (Figs 11, 21–28) . 17
6 Pseudorostrum long, 1/3 of total carapace length and armed with long spines (Figs 12–13) 7
– Pseudorostrum less than 1/3 of total carapace length and unarmed (Figs 4–6, 14–20) 8
7 Sides of carapace unarmed; eyelobe short and rounded (Fig. 12) ***aculeata*** sp. nov. (p. 221)
– Carapace with spines all over; eyelobe narrow and as long as pseudorostrum (Fig. 13) ***echinata*** sp. nov. (p. 223)
8 Pseudorostrum short, not more than 1/8 of total carapace length; eyelobe not elongate (Figs 14–17) 9
– Pseudorostrum fairly long, at least 1/6 of total carapace length; eyelobe long and narrow (Figs 4–6, 18–20) 12
9 Carapace serrated dorsally but without spines (Figs 14, 15) 10
– Carapace with mid-dorsal spines (Figs 16, 17) 11
10 Eyelobe rounded and serrated; posterior pereonites with a transverse row of spines (Fig. 14). ***concinna*** sp. nov. (p. 224)
– Eyelobe narrowed and smooth; pereonites without spines rows (Fig. 15) ***exstans*** sp. nov. (p. 225)
11 A single row of about 8 mid-dorsal spines on carapace; eyelobe narrowed (Fig. 16) ***dayae*** sp. nov. (p. 226)
– Two rows set close together of numerous spines mid-dorsally on carapace; eyelobe broad at base (Fig. 17) ***subducta*** sp. nov. (p. 227)
12 Carapace without spines or serrations, eyelobe much shorter than pseudorostrum (Fig. 18) ***angustata*** sp. nov. (p. 228)
– Carapace with at least one row of mid-dorsal spines (Figs 4–6, 19, 20) 13
13 Pleon unarmed (Fig. 4) ***gracillima*** Calman, 1905
– Pleon with longitudinal spine rows or serrations (Figs 5, 6, 19, 20) 14
14 Spines in a single row mid-dorsally on carapace (Figs 5, 19) 15
– Spines set in two rows mid-dorsally at least on the hind part of the carapace (Figs 6, 20) 16
15 About 5 mid-dorsal spines on the carapace; bases of posterior pereopods and uropods unarmed (Fig. 19). ***erecta*** sp. nov. (p. 229)
– 15 or more mid-dorsal spines on carapace, bases of posterior pereopods and uropods with spine rows (Fig. 5) ***egregia*** Hansen, 1920
16 Some spines on sides of carapace and transverse spine rows on pereonites; first antenna long (Fig. 6) ***antipai*** (Bacescu & Muradian, 1974)
– Sides of carapace unarmed and pereonites without transverse rows of spines, first antenna much shorter (Fig. 20) ***formosa*** sp. nov. (p. 231)
17 Eyelobe narrowed, as long as pseudorostrum (Figs 11, 21–23) 18
– Eyelobe rounded or not much elongated, distinctly shorter than the pseudorostrum (Figs 24–28) 21
18 About 5 or fewer spines mid-dorsally on the carapace (Fig. 11) ***acuminata*** sp. nov. (p. 220)
– More than 10 spines mid-dorsally on carapace (Figs 21–23) 19
19 Two distinct rows of many hook-shaped spines mid-dorsally on the carapace; there are spines on the carapace border above as well as below the antero-lateral angle (Fig. 21) ***bishopi*** sp. nov. (p. 233)
– Spines mid-dorsally on the carapace fewer and irregularly doubled; no spines on carapace border above antero-lateral angle (Figs 22, 23) 20

20 Carapace elongate, about twice as long as deep; pseudorostrum truncate, not projecting forward much beyond front of carapace (Fig. 22) ***cristata*** sp. nov. (p. 234)
– Carapace much less than twice as long as deep; pseudorostrum pointed, projecting forward well beyond front edge of carapace (Fig. 23) ***longisipho*** sp. nov. (p. 235)
21 Pseudorostrum long and pointed, almost 1/3 of total carapace length (Fig. 24) ***spicata*** sp. nov. (p. 235)
– Pseudorostrum shorter, not more than 1/6 of total carapace length (Figs 25–28). 22
22 Carapace with more than 12 mid-dorsal spines or serrations (Fig. 25) ***polita*** sp. nov. (p. 237)
– Carapace with not more than 12 mid-dorsal spines (Figs 26–28) 23
23 Carapace with mid-dorsal spines prominent; pleon and uropods comparatively stout (Fig. 26) ***meridionalis*** sp. nov. (p. 238)
– Carapace with mid-dorsal spines not prominent; pleon and uropods comparatively slender (Figs 27, 28) 24
24 Carapace slightly arched dorsally and with a row of about 12 irregular spines; peduncle of uropod $1\frac{1}{4}$ as long as endopod (Fig. 27) ***compacta*** sp. nov. (p. 240)
– Carapace with few or no spines dorsally but raised at hind end; peduncle of uropod $1\frac{1}{2}$ as long as endopod (Fig. 28) ***decipiens*** sp. nov. (p. 240)

Genus *ATLANTOCUMA* Bacescu and Muradian, 1974

General appearance similar to *Iphinoe*, with 5 free pereonites, the first almost fused to the carapace. Mandible boat-shaped. Telson not separated. No pleopods in either sex. Uropodal endopod one-segmented. Only the first pair of pereopods with exopods in the female, pereopods 1–4 in the male. Maxilliped 1 without the branchial elements. Maxilliped 3 with long basis not distally widened.

Bacescu and Muradian were uncertain about the systematic position of the genus, stressing its bodotriid characters apart from the lack of pleopods. The lack of a free telson and of pleopods seem to place it in the Nannastacidae and perhaps it is best left there to avoid confusion between family diagnoses. However, from its general appearance and the shape of the mouthparts it is most likely an aberrant member of the Bodotriidae.

Atlantocuma benguelae Bacescu and Muradian, 1974

MATERIAL. AII60-247: 1 ad. ♂, 42 imm. ♂♂, 49 ad. ♀♀, 25 imm. ♀♀.

DISTRIBUTION. The first record of this species was from 4893 m depth south of Cape Town. It is now recorded from 5223 m off the Argentine coast. In the adult male the pseudorostrum is abruptly truncate.

Atlantocuma tenuis sp. nov
(Fig. 29)

MATERIAL. MBAUK-50: 1 ad. ♀, 1 imm. ♀. 65: 1 imm. ♀, 2 juv. IOS-7709 # 72: 1 imm. ♀. 7709 # 73: 4 ad. ♀♀, 2 juv. SMBA-ES4: 1 imm. ♂, 3 ad. ♀♀. ES10: 8 imm. ♂♂, 14 ad. ♀♀, 34 imm. ♀♀, 8 juv. ES12: 4 ad. ♂♂, 14 imm. ♂♂, 14 ad. ♀♀, 19 imm. ♀♀, 7 juv. BIOGAS I-DS13: 1 imm. ♀, 1 juv. POLYGAS-DS15: 39 imm ♀♀. DS18: 75 imm. ♀♀. BIOGAS II-DS31: 1 imm. ♀. BIOGAS III-DS50: 2 ad. ♀♀. BIOGAS IV-DS51: 3 ad. ♀♀. DS52: 1 ad. ♀, 1 imm. ♀. BIOGAS V-DS66: 2 imm. ♂♂, 3 ad. ♀♀, 6 imm. ♀♀. BIOGAS VI-DS79: 4 ad. ♂♂, 5 imm. ♂♂, 3 ad. ♀♀, 3 imm. ♀♀, 2 juv. DS86: 40 imm. ♀♀. DS87: 7 imm. ♀♀. CP09: 7 ad. ♀♀. CP23: 1 imm. ♀, 1 juv. *Atlantis* 264-G_1 # 1: 1 imm. ♂. AII12-66: 1 imm. ♂, 1 ad. ♀, 1 imm. ♀. 70: 6 ad. ♀♀. Ch50-76: 1 ad. ♀. 83: 1 juv. 84: 1 imm. ♂, 5 ad. ♀♀. 85: 3 imm. ♂♂, 11 ad. ♀♀, 6 imm. ♀♀. AII17-92: 1 ad. ♀. 93: 1 ad. ♀. Ch58-103: 1 imm. ♂, 1 ad. ♀. AII24-125: 2 imm. ♂♂, 4 ad. ♀♀, 1 imm. ♀, 1 juv. 126: 1 ad. ♂, 3 imm. ♂♂, 5 ad. ♀♀. AII30-131: 2 ad. ♂♂, 16 imm. ♂♂, 23 ad. ♀♀, 19 imm. ♀♀, 5 juv. AII31-155: 2 imm. ♂♂, 1 ad. ♀, 2 imm. ♀♀, 2 juv. 156: 1 ad. ♂, 4 imm. ♂♂, 6 ad. ♀♀. 162: 2 ad. ♀♀. 169: 2 ad. ♀♀. AII40-175: 1 imm. ♀, 1 juv. AII42-198: 1 ad. ♀. 201: 2 imm. ♂♂, 1 ad. ♀. 9 imm. ♀♀. AII60-239: 3 ad. ♂♂, 6 imm. ♂♂, 312 ad. ♀♀, 212 imm. ♀♀. 242: 1 juv. 245: 13 ad. ♂♂, 33 imm. ♂♂, 174 ad. ♀♀, 126 imm. ♀♀. Kn25-287: 3 imm. ♀♀. 191: 1 imm. ♀. 293: 1 imm. ♂, 13 ad. ♀♀, 6 juv. 295: 2 juv. 297: 4 imm. ♀♀. 299: ad. ♂, 1 imm. ♂, 12

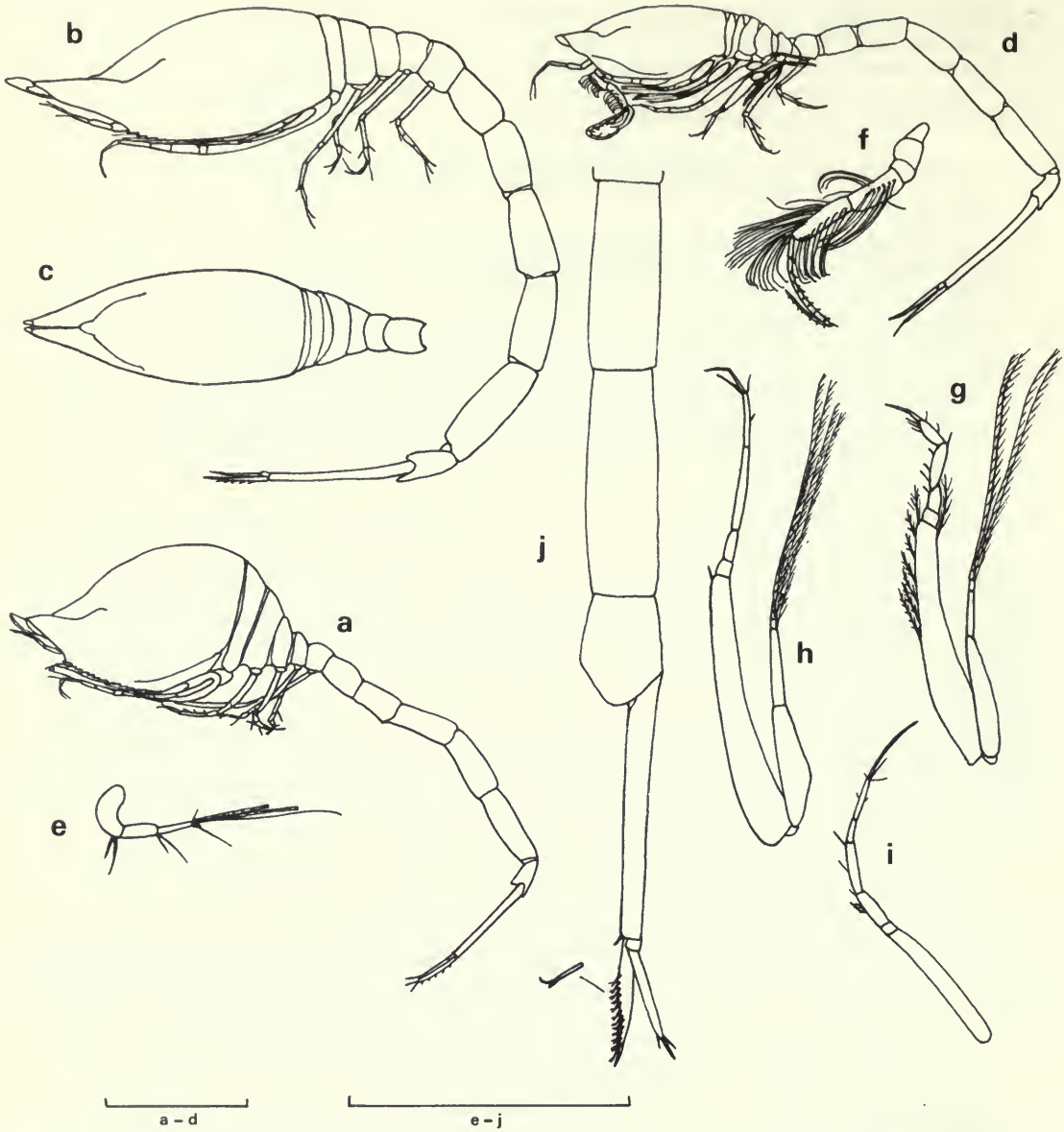

Fig. 29 *Atlantocuma tenuis*, (a) ovigerous ♀ from side; (b) adult ♀ from side; (c) carapace and pereon of adult ♀ from above; (d) adult ♂ from side; (e) ♀ antenna 1; (f) ♂ antenna 2; (g) ♀ maxilliped 3; (h) pereopod 1; (i) pereopod 2; (j) uropod and end of pleon.

ad. ♀♀, 15 imm. ♀♀. 301: 5 ad. ♂♂, 10 imm. ♂♂, 6 ad. ♀♀, 24 imm. ♀♀. 303: 3 ad. ♀♀, 1 juv. Ch106-318: 1 imm. ♂, 2 imm. ♀♀, 1 juv. 334: 30 ad. ♂♂, 7 imm. ♂♂, 45 ad. ♀♀, 4 imm. ♀♀. Kn35-340: 79 ad. ♂♂, 4 imm. ♀♀, 61 ad. ♀♀, 3 imm. ♀♀.

DESCRIPTION. Ovigerous female, length 4·6 mm: carapace (Fig. 29a) smooth, strongly arched dorsally, about $1\frac{1}{2}$ as long as high, laterally compressed; pseudorostrum not very long, pointed, siphons short; antero-lateral angle not prominent, marked by a blunt spine, with a row of serrations on the lower margin behind; eyelobe fairly large, pointed at front, without lenses. Pereon somites smooth, all distinct, the first two deep, not differing much in length. Pleon long and slender without spines or serrations.

Antenna 1 (Fig. 29e) of moderate length, its basal segment strongly curved, much shorter than the subequal second and third segments together; the main flagellum has two aesthetascs. Maxilliped 3 (Fig. 29g) with basis very long, about three times as long as remaining segments together; carpus about as long as ischium and merus together and distinctly longer than propodus; dactyl short and narrow with a terminal claw. Pereopod 1 (Fig. 29h) very slender with basis distinctly longer than remaining segments together, carpus about twice as long as ischium and merus together and much longer than the propodus, which is about twice as long as the narrow dactyl. Pereopod 2 (Fig. 29i) longer than pereopods 3–5, with basis shorter than remaining segments together; carpus about as long as ischium and merus together, more than twice as long as the propodus and a little longer than the dactyl. Only the first pereopods have an exopod. Uropods (Fig. 29j) with basis distinctly longer than pleonite 5 and nearly three times as long as the endopod, which is one-segmented with a distal row of 12–13 compound spines and a little longer than the two-segmented exopod.

Adult female, length 6·6 mm: similar otherwise to ovigerous female, but carapace (Fig. 29b, c) proportionately longer and less deep, nearly $2\frac{1}{2}$ as long as high; the pseudorostrum is proportionately longer and there are fewer serrations on the infero-lateral borders; there is less difference in height between the first two and the last three pereonites.

Adult male, length 4·2 mm: carapace (Fig. 29d) less arched than in ovigerous female and infero-lateral borders without serrations. Antenna 2 (Fig. 29f) with brushes of long fine setae on last two segments of peduncle; flagellum short, not reaching as far back as rear of carapace, about 11-segmented. Exopods are present on pereopods 1–4. The uropod peduncles are proportionately longer than in the female.

The difference in carapace shape described above between smaller ovigerous and larger non-ovigerous females seems to be consistent and it therefore appears possible that the larger females acquire their more elongated carapace at a moult subsequent to brood release.

TYPE LOCALITY. 36° 49′ S, 35° 15·4′ W, 1661–1679 m. Type material deposited in the British Museum (Natural History). Holotype 1982 : 327 : 1, allotype 1982 : 328 : 1, paratypes 1982 : 329 : 30.

REMARKS. *A. tenuis* is generally similar to the type species but has a less truncate and more pointed pseudorostrum in either sex.

DISTRIBUTION. Widespread in the North and South Atlantic both horizontally and vertically between 587 and 5000 m depth.

Genus ***CUMELLOPSIS*** Calman, 1905

Carapace ovoid, without mid-dorsal spines. Eyelobe rudimentary, without eyes. Mandibles normal. Maxilliped 2 with 7 segments.

Although *Cumellopsis* has a rather distinct facies which is different from that of any species of *Cumella,* it is at present impossible to give a satisfactory diagnosis of the genus which will separate it from the latter. It is not known if the number of segments in the second maxilliped is always less than 7 in *Cumella.* Bacescu and Muradian (1977) provide a key to the genera of the Nannastacidae in which *Cumellopsis* and *Platycuma* are separated from *Cumella* by a shorter second antennal flagellum in the adult male. However, while this holds good for *Platycuma*, in some of the species of *Cumellopsis* at least, the second antennal flagellum of fully adult males reaches back beyond the carapace, in *C. helgae* to the hind end of the pleon.

Cumellopsis helgae Calman, 1905

MATERIAL. MBAUK-56: 1 ad. ♂. 63: 1 imm. ♂, 4 imm. ♀♀. 66: 1 ad. ♀. SMBA-ES4: 3 ad. ♂♂, 7 imm. ♂♂, 21 imm. ♀♀. ES10: 1 imm. ♂. ES12: 3 imm. ♂♂, 3 ad. ♀♀, 3 imm. ♀♀. ES18: 1 ad. ♀. ES20: 1 imm. ♂, 1 juv. ES22: 1 imm. ♂, 1 imm. ♀. ES58: 1 imm. ♂. SBC67: 1 imm. ♀. ES137: 1 imm. ♀. ES147: 1 imm ♂, 1 ad. ♀, 1 imm. ♀. *Thalassa* 73-Z421: 1 ad. ♀. Z435: 1 ad. ♂. Z441: 1 imm. ♀, 2 juv. POLYGAS-DS15: 1 ad. ♂, 7 ad. ♀♀, 1 imm. ♀. DS16: 1 imm. ♀. DS18: 3 ad. ♂♂, 4 ad. ♀♀, 4 imm. ♀♀. DS26:

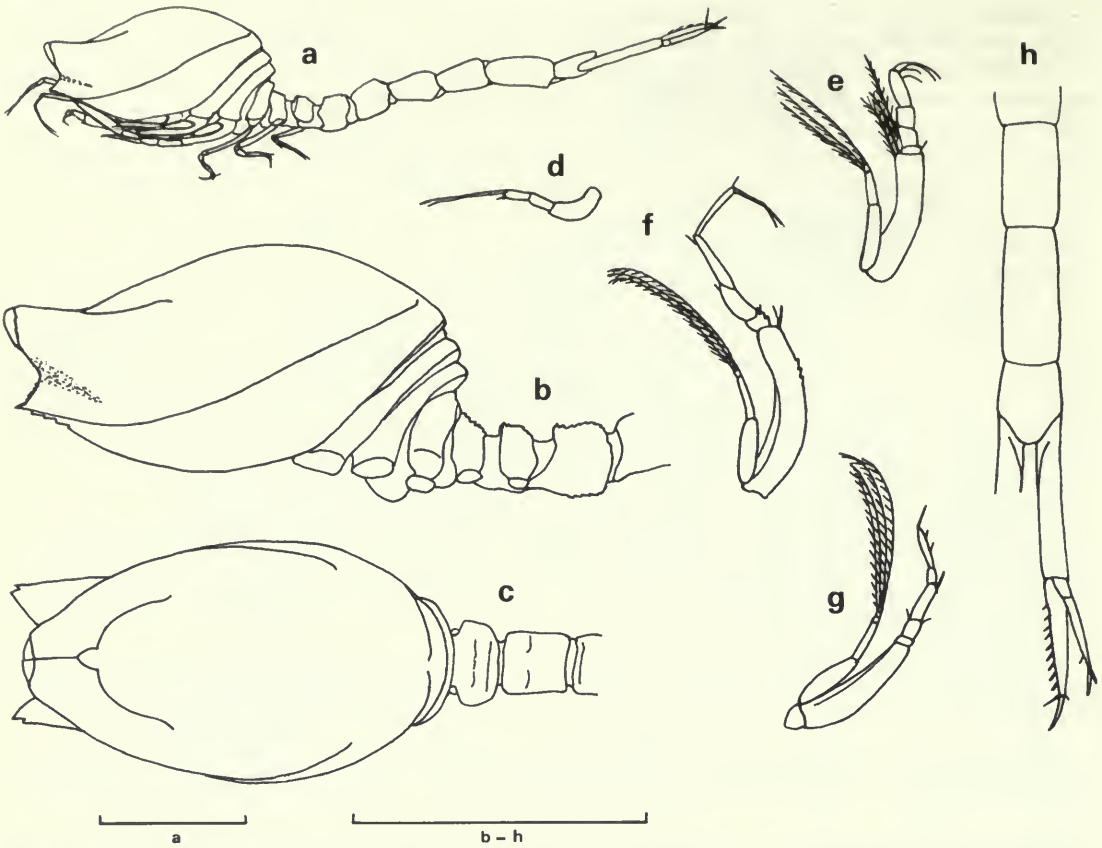

Fig. 30 *Cumellopsis puritani* ♀, (a) lateral view; (b) carapace and pereon from side; (c) carapace and pereon from above; (d) antenna 1; (e) maxilliped 3; (f) pereopod 1; (g) pereopod 2; (h) uropod and end of pleon.

1 imm. ♂. BIOGAS II-DS30: 1 imm. ♂. DS31: 2 imm. ♂♂, 4 ad. ♀♀. DS33: 5 imm. ♂♂, 10 imm. ♀♀, 2 juv. DS34: 1 imm. ♀. BIOGAS III-DS35: 1 ad. ♂, 1 juv. DS41: 1 imm. ♂, 4 ad. ♀♀, 1 imm. ♀. DS49: 1 imm. ♂. BIOGAS IV-DS51: 2 ad. ♀♀. DS52: 1 imm. ♂, 4 ad. ♀♀. DS62: 1 imm. ♀. BIOGAS VI-DS86: 5 imm. ♂♂, 2 ad. ♀♀, 5 imm. ♀♀, 1 juv. DS87: 1 imm. ♂, 2 imm. ♀♀, 3 juv. CP23: 3 imm. ♂♂, 2 imm. ♀♀. CP25: 9 ad. ♀♀, 6 juv. *Atlantis* 283-Slope # 4: 1 imm. ♀. Ch50-87: 5 ad. ♂♂, 10 imm. ♂♂, 112 ad. ♀♀, 120 imm. ♀♀. Ch58-96: 29 imm. ♂♂, 24 ad. ♀♀, 37 imm. ♀♀, 1 juv. 105: 3 imm. ♂♂, 3 ad. ♀♀, 3 imm. ♀♀. Ch88-207: 26 imm. ♂♂, 15 ad. ♀♀, 30 imm. ♀♀, 7 juv. Ch106-321: 1 ad. ♂, 3 imm. ♂♂, 2 ad. ♀♀, 2 imm. ♀♀. Kn35-346: 29 imm. ♂♂, 19 ad. ♀♀, 21 imm. ♀♀, 61 juv.

REMARKS. As noted above, the male second antennal flagellum is long and slender, reaching back beyond the hind end of the pleon and this seems to be a character separating it from *C. puritani,* in which the flagellum reaches only to the hind end of the pereon.

DISTRIBUTION. Previously recorded from 699 m west of Ireland and 208 to 924 m south and north-west of Iceland and the Faroes, the present records show it to be widespread on both sides of the northern North Atlantic between 400 and 4106 m depth.

Cumellopsis puritani Calman, 1906
(Fig. 30)

MATERIAL. MBAUK-56: 1 ad. ♀. AII59-211: 2 ad. ♂♂, 4 imm. ♂♂, 14 ad ♀♀, 2 juv.

DISTRIBUTION. Recorded from the Mediterranean by Calman in 950–1100 m depth, and by

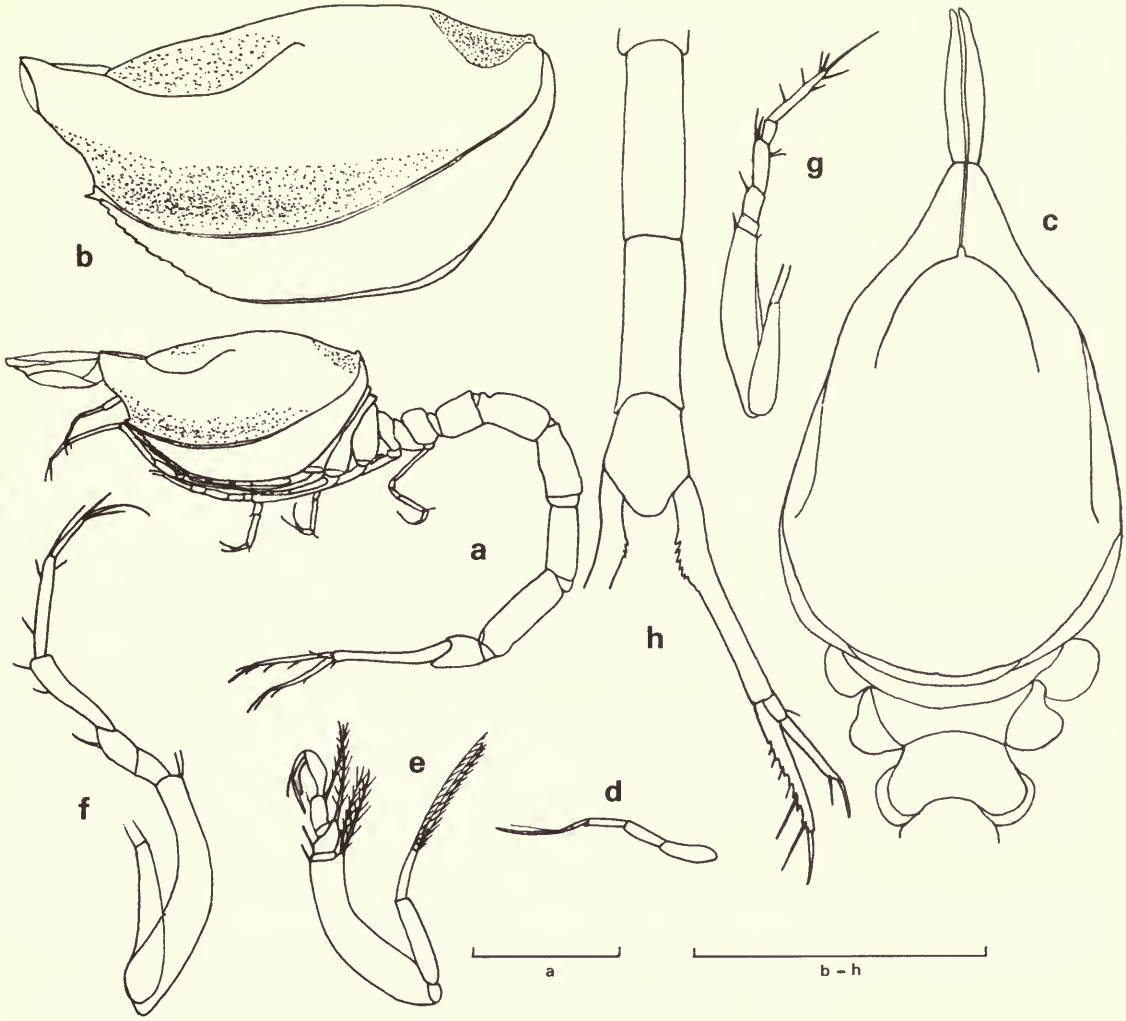

Fig. 31 *Cumellopsis bicostata* ♀, (a) lateral view; (b) carapace and pereon from side; (c) carapace and pereon from above; (d) antenna 1; (e) maxilliped 3; (f) pereopod 1; (g) pereopod 2; (h) uropod and end of pleon.

Reyss (1972, 1973) in 2110 m and 2090 m, it is again recorded from the Mediterranean in 509 m and from Biscay in 641 m.

Cumellopsis bicostata sp. nov.
(Fig. 31)

Material. IOS-7709 # 73: 1 imm. ♂, 1 imm. ♀. POLYGAS-DS21: 3 ad. ♂♂, 1 ad. ♀. DS22: 1 imm. ♂. AII31-162: 1 ad. ♂, 1 ad. ♀. 167: 2 ad. ♂♂, 4 imm. ♂♂, 14 ad. ♀♀, 2 imm. ♀♀. AII60-239: 4 ad. ♂♂, 22 imm. ♂♂, 106 ad. ♀♀, 52 imm. ♀♀. Kn25-239: 1 ad. ♂, 2 imm. ♂♂, 51 ad. ♀♀, 34 imm. ♀♀. 295: 2 imm. ♂♂, 8 ad. ♀♀. 297: 1 ad. ♀, 1 imm. ♀. 301: 2 ad. ♂♂, 2 imm. ♂♂, 3 imm. ♀♀. 303: 1 imm. ♂, 1 imm. ♀.

Description. Adult female, length 5·2 mm: carapace (Fig. 31a-c) well calcified, less than twice as long as deep and fairly broad, a little raised postero-dorsally, with well-defined ridge on either side running back from the antero-lateral angle to join its fellow dorsally near

the hind end; above the ridge on either side is a shallow depression; pseudorostrum fairly long with long siphons; the antero-lateral angle not prominent, defined by a strong tooth with a few serrations behind; eyelobe very small. Pereon and pleon somites without spines or serrations, the pleon slender.

Antenna 1 (Fig. 31d) fairly long with the three segments of the peduncle fairly narrow and decreasing in length distally only slightly. Maxilliped 3 (Fig. 31e) with basis much longer than remaining segments together, the merus broad with its distal upper end prolonged; the carpus and propodus about equal in length; the propodus broadened and nearly twice as long as the narrow dactyl. Pereopod 1 (Fig. 31f) unarmed, with its basis much shorter than remaining segments combined, its carpus about as long as the propodus and a little longer than the ischium and merus together; the dactyl is short and narrow. Pereopod 2 (Fig. 31g) with basis about as long as remaining segments together, its carpus about twice as long as the propodus and about 2/3 the length of the dactyl, which is not very narrow. Uropod (Fig. 31h) with basis about 1½ as long as pleonite 5, somewhat curved, with a bulge on its inner edge near the base bearing a few serrations; the endopod is about 3/5 as long as the peduncle, with some serrations on its inner edge and some spines which are longer distally; the exopod is distinctly shorter than the endopod.

The adult male resembles the female in general aspect. The flagellum of antenna 2 is fairly short. The uropodal exopod is shorter in proportion to the endopod and the bend in its peduncle is less pronounced.

TYPE LOCALITY. 8° 58′ N, 54° 04.3′ W, 1456–1518 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 330 : 1, allotype 1982 : 331 : 1, paratypes 1982 : 332 : 20.

REMARKS. *Cumellopsis bicostata* differs from *C. helgae* and resembles *C. puritani* in the presence of a well defined and sharp ridge on either side of the carapace. In *C. puritani* the antero-lateral angle is much more pronounced, reaching nearly as far forward as the front of the pseudorostrum, the eyelobe is larger and the uropod peduncle is straighter, without inner serrations.

DISTRIBUTION. The species has been found to be fairly widespread between 500 and 4144 m from off the Argentine and Brazil coasts in the south-west and west tropical Atlantic and off Surinam and from west of Scotland and Biscay in the North Atlantic.

Cumellopsis laevis sp. nov.
(Fig. 32)

MATERIAL. IOS-6696: 2 imm. ♂♂, 3 ad. ♀♀, 2 imm. ♀♀. 6709: 4 imm. ♀♀. SBMA-ES129: 1 imm. ♂. BIOGAS V-DS66: 1 imm. ♂, 1 imm. ♀, 1 juv. DS67: 3 ad. ♀♀.

DESCRIPTION. Adult female, length 4·9 mm: carapace (Fig. 32a, b) well calcified, pearly white, without lateral ridges or furrows except just above the antero-lateral angle, nearly twice as long as high; pseudorostrum fairly long, somewhat truncated, with some crenulations in front; the eyelobe small; antero-lateral angle well defined by a strong spine with several others decreasing in size behind it. Pereon and pleon unarmed, the pleon slender.

Antenna 1 (Fig. 32c) slender, not very long, the basal segment nearly as long as the second and third together, the second nearly twice as long as the third. Maxilliped 3 (Fig. 32d) with basis curved, distinctly longer than remaining segments together, the propodus longer than the subequal carpus or dactyl. Pereopod 1 (Fig. 32e) with the basis distally narrow, distinctly shorter than remaining segments together, the carpus and propodus nearly equal in length and each much longer than the merus; the dactyl short. Pereopod 2 (Fig. 32f) with basis comparatively short and broad at the base, the carpus more than twice as long as the propodus and longer than the merus but a little shorter than the slender dactyl. Uropod (Fig. 32g) with peduncle slender, straight, less than 1½ as long as pleonite 5, nearly twice as long

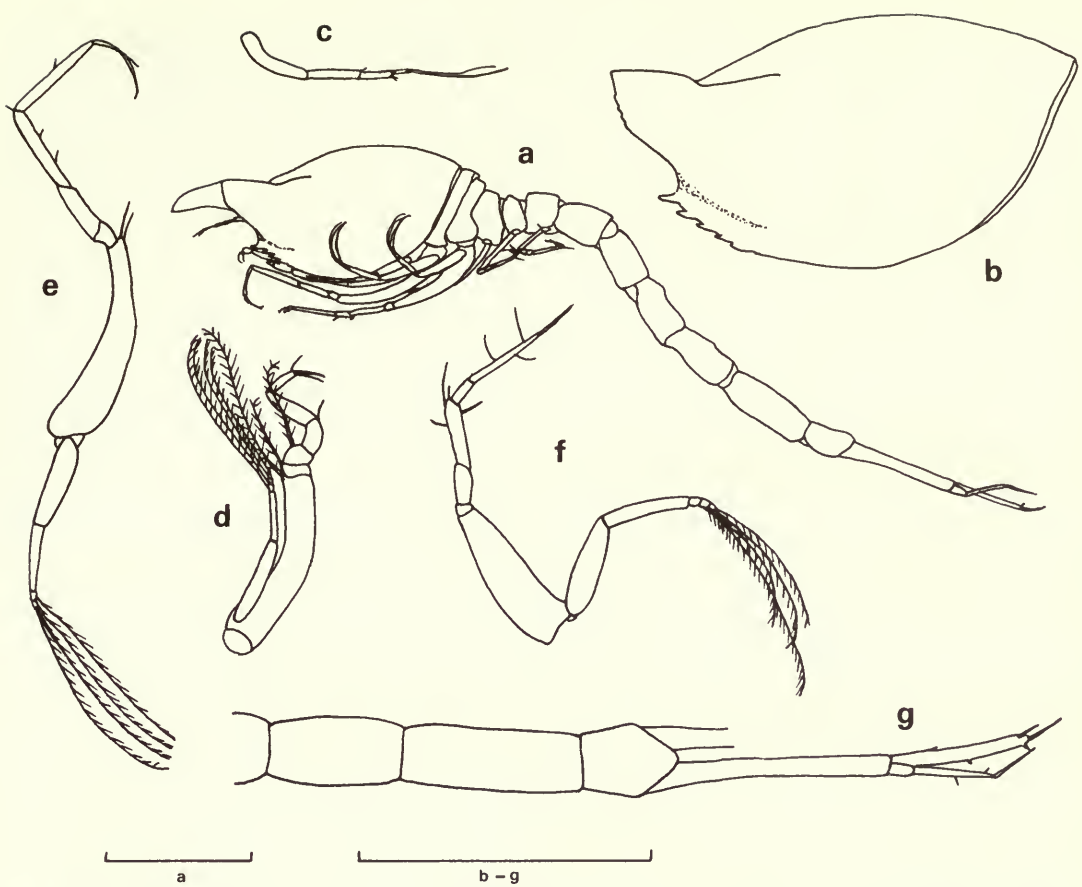

Fig. 32 *Cumellopsis laevis* ♀, (a) lateral view; (b) carapace from side; (c) antenna 1; (d) maxilliped 3; (e) pereopod 1; (f) pereopod 2; (g) uropod and end of pleon.

as the endopod, which has only a few short spines on its inner edge and is much longer than the narrower exopod.

Adult male unknown.

TYPE LOCALITY. 28° 06′ N, 13° 28′ W, 1780 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 333 : 1, paratypes 1982 : 334 : 3.

REMARKS. *Cumellopsis laevis* differs from the three other species of the genus found in these collections by the absence of lateral ridges or furrows on its carapace. It seems to be generally similar to *C. est-africana* (Bacescu and Muradian) but the latter is known only from the adult male.

DISTRIBUTION. Recorded from Biscay and the Canary Islands in depths between 1780 and 4150 m.

Genus ***PLATYCUMA*** Calman, 1905

Generally resembling *Cumellopsis* but sometimes more flattened dorso-ventrally and always with the forepart of the gut spirally coiled.

Platycuma holti Calman, 1905

MATERIAL. MBAUK-50: 6 ad. ♀♀, 9 imm. ♀♀. 66: 4 ad. ♂♂, 5 ad. ♀♀. IOS-7709 # 62: 5 ad. ♂♂, 2 ad.

♀♀, 1 juv. 7709 # 72: 2 imm. ♂♂, 3 ad. ♀♀, 7 juv. 7709 # 73: 3 ad. ♂♂, 1 imm, ♂. 12 ad. ♀♀. 7709 # 85: 3 ad. ♂♂, 6 ad. ♀♀, 1 imm. ♀. SMBA-ES4: 1 imm. ♀. ES12: 2 ad. ♂♂, 4 ad. ♀♀, 3 imm. ♀♀, 4 juv. BIOGAS I-DS14: 2 juv. POLYGAS-DS15: 2 imm. ♀♀. DS16: 2 ad. ♀♀, 1 juv. DS18: 1 juv. DS26: 1 imm. ♀. BIOGAS II-DS31: 19 imm. ♂♂, 6 ad. ♀♀, 14 imm. ♀♀, 125 juv. BIOGAS III-DS41: 3 ad. ♂♂, 6 imm. ♂♂, 10 ad. ♀♀, 24 imm. ♀♀. DS49: 1 ad. ♀. DS50: 1 imm. ♀. BIOGAS IV-DS51: 2 ad. ♂♂, 1 imm. ♂, 2 ad. ♀♀, 6 juv. BIOGAS V-DS66: 2 imm. ♂♂, 2 ad. ♀♀, 4 imm. ♀♀. BIOGAS VI-DS74: 3 imm. ♂♂, 1 ad. ♀, 4 imm. ♀♀, 1 juv. DS79: 1 juv. CP09: 1 imm. ♀. CP25: 1 imm. ♀. *Atlantis* 273-GH # 3: 1 imm. ♂. AII12-62: 1 ad. ♀. 64: 1 imm. ♂, 5 ad. ♀♀, 92 imm. ♀♀, 1 juv. 66: 1 ad. ♀, 5 imm. ♀♀. 70: 3 ad. ♂♂, 1 imm. ♂, 1 ad. ♀, 1 imm. ♀. 72: 1 imm. ♂, 5 ad. ♀♀, 2 imm. ♀♀. Ch50-76: 17 imm. ♂♂, 20 ad. ♀♀, 23 imm. ♀♀. 84: 2 imm. ♂♂, 1 imm. ♀. AII24-125: 1 ad. ♀, 1 imm. ♀. AII30-131: 1 imm. ♀. AII31-144: 1 imm. ♂, 1 ad. ♀, 1 imm. ♀. 155: 6 imm. ♂♂, 5 ad. ♀♀, 6 imm. ♀♀. 156: 1 ad. ♂, 11 imm. ♂♂, 8 ad. ♀♀, 9 imm. ♀♀, 8 juv. AII60-239: 1 ad. ♂, 7 ad. ♀♀, 2 imm. ♀♀. 240: 4 ad. ♂♂, 5 imm. ♂♂, 8 ad. ♀♀, 1 juv. 262: 3 imm. ♂♂, 2 imm. ♀♀, 1 juv. 264: 1 ad. ♀. Kn25-291: 1 ad. ♀. 293: 1 imm. ♀. 295: 1 imm. ♀. 299: 1 imm. ♂, 10 ad. ♀♀, 6 imm. ♀♀. 301: 1 ad. ♀, 14 juv. 303: 3 imm. ♀♀, 3 juv. Ch106-313: 14 juv. 321: 1 ad. ♂, 9 imm. ♂♂, 11 ad. ♀♀, 16 imm. ♀♀. 323: 3 imm. ♂♂, 4 ad. ♀♀, 5 imm. ♀♀, 1 juv. 328: 1 imm. ♀. 334: 7 imm. ♂♂, 1 ad. ♀, 3 imm. ♀♀, 5 juv. Kn35-340: 1 ad. ♂, 1 imm. ♂.

REMARKS. Zimmer (1943, 1980) described *Platycuma marginalis* from a single young male found in 2795 m off the north-east coast of the U.S.A. and suggested that Fage's two specimens from Biscay did not belong to *P. holti* but possibly to *P. marginalis.*

Although a considerable number of specimens is now available, I have not found it possible to confirm the existence of *P. marginalis.* In the collections from Ch106 Sta. 323 and BIOGAS III Sta. DS41, two forms may tentatively be distinguished among mature and subadult females differing as follows:

A	**B**
Pseudorostrum reaching about as far forward as antero-lateral angle.	Pseudorostrum not reaching as far forward as antero-lateral angle.
Antero-lateral angle relatively acute, with distinct teeth.	Antero-lateral angle relatively obtuse, teeth often indistinct.
Dorsal somite ridges relatively strongly toothed.	Dorsal somite ridges relatively weakly toothed.
Uropod peduncle relatively slender.	Uropod peduncle relatively stout.
Posterior margins of pleonite 6 almost straight.	Posterior margins of pleonite 6 forming an angle.

Specimens from Ch106 Sta. 321 all resemble form **A.** Mature and immature males show considerable variation but are not readily divisible into forms; however, the mature males are not easily recognizable as belonging to Calman's species. I do not consider Fage's male to differ sufficiently from Calman's to be regarded as separate. Contrary to his suggestion, it is more likely that Calman's type specimen was fully mature while Fage's male was in the previous moult stage. It is not completely true that, as stated by Zimmer (1980), young males still have entirely female characters. Apart from the different stages of development of second antennae and pereopodal exopods, the shape of the carapace and other characters may differ from that of females in males one or two moults before maturity and these stages can therefore not be compared in all respects with females. The two forms **A** and **B** do not correspond respectively to Fage's female or to the immature male described as *P. marginalis* by Zimmer.

I believe that only one species, *P. holti,* is present and that *P. marginalis* cannot be considered separate, although some doubts must still remain.

DISTRIBUTION. Recorded by Calman from west of Ireland in 688 m and Fage (1929) from Biscay in 4380 m, it is now found to be widespread on both sides of the North and tropical Atlantic and from off the Argentine coast, between 1000 and 4825 m.

Platycuma sandersi Jones, 1973

MATERIAL. IOS-6709: 2 imm. ♂♂, 1 imm. ♀, 2 juv. SMBA-ES10: 4 imm. ♀♀. POLYGAS-DS15: 1 imm. ♀. DS20: 1 ad. ♂, 5 ad. ♀♀, 4 juv. DS21: 6 ad. ♀♀. DS22: 1 ad. ♀. BIOGAS IV-DS51: 1 imm. ♂. DS55: 9 juv. BIOGAS V-DS66: 7 imm. ♂♂, 10 imm. ♀♀. DS67: 4 imm. ♂♂, 2 imm. ♀♀. Ch50–85: 34 ad. ♂♂, 36 ad. ♀♀, 2 imm. ♀♀. AII31-142: 1 imm. ♀. 144: 1 imm. ♀. 156: 1 imm. ♂, 1 ad. ♀. 167: 4 imm. ♂♂, 7 ad. ♀♀, 5 imm. ♀♀. Kn25–287: 1 imm. ♀. 288: 1 imm. ♂, 1 imm. ♀. 291: 1 ad. ♀, 1 imm. ♀, 2 juv. Ch106-321: 3 ad. ♀♀, 1 juv. 323: 1 ad. ♂, 1 ad. ♀, 1 juv. 334: 1 ad. ♂, 2 imm. ♂♂, 20 ad. ♀♀, 29 imm. ♀♀, 2 juv. Kn35–340: 2 ad. ♀♀, 1 juv.

REMARKS. In this species there is a distinct keel, not shown in Fig. 6 (Jones, 1973), running backwards on either side from the antero-lateral angle not quite to the hind end of the carapace. This keel is not present in *P. hessleri.* The adult male, not previously known, resembles the male of *P. holti* in the general shape of its carapace and differs from the male of *P. hesserli,* but is noticeably smaller, less than 4 mm in length compared with more than 4 mm in the adult male of *P. holti.* As in the female the exopod of the uropod is comparatively long, nearly as long as the endopod.

DISTRIBUTION. Now recorded from both sides of the Atlantic from the tropical region northwards between 943 and 5000 m.

Platycuma hessleri Jones, 1973
(Fig. 33)

MATERIAL. IOS-6704: 1 imm. ♂. 6711: 1 imm. ♀. 6714: 1 ad. ♀. 7709 # 72: 3 ad. ♀♀. 7709 # 73: 4 imm. ♀♀. 7709 # 85: 1 imm. ♂, 1 ad. ♀. POLYGAS-DS21: 1 ad ♂, 1 imm. ♀, 2 juv. BIOGAS II-DS31: 1 ad. ♀. BIOGAS III-DS41: 1 imm. ♂, 3 ad. ♀♀, 2 imm. ♀♀. BIOGAS V-DS66: 1 imm. ♂, 1 imm. ♀, 2 juv. DS67: 2 imm. ♀♀. BIOGAS VI-DS76: 1 imm. ♀. DS79: 1 imm. ♂, 1 imm. ♀. AII12-64: 1 ad. ♂, 5 imm. ♂♂, 26 ad. ♀♀, 6 imm. ♀♀, 11 juv. 66: 1 ad. ♂, 1 imm. ♂, 5 ad. ♀♀, 1 juv. 72: 2 ad. ♂♂, 1 ad. ♀. AII31-155: 2 ad. ♂♂, 1 imm. ♂, 6 ad. ♀♀. 156: 2 ad. ♂♂, 15 imm. ♂♂, 13 ad. ♀♀, 8 imm. ♀♀, 9 juv. AII42-195: 1 ad. ♀, 5 juv. Kn25-291: 1 imm. ♂. 306: 2 ad. ♀♀, 2 juv. Ch106-321: 5 imm. ♂♂, 1 ad. ♀, 5 imm. ♀♀, 1 juv. 323: 1 imm. ♂, 4 ad. ♀♀, 1 imm. ♀. Kn35-340: 1 ad. ♀, 2 juv.

REMARKS. The only notable difference in a larger female, length 6·7 mm, and the original description of an adult female, length 3·8 mm, is in the length and shape of the uropods (Fig. 33g). In the larger female, these are much longer than the last two pleonites together and the peduncles and endopod have distinct inner serrations, with some outer serrations at the base of the peduncle, which is somewhat tapered.

DISTRIBUTION. Widespread on both sides of the North and South Atlantic and in the tropical region between 2129 and 4715 m.

Platycuma candida sp. nov.
(Fig. 34)

MATERIAL. POLYGAS-DS20: 1 ad. ♀. BIOGAS III-DS41: 4 ad. ♂♂, 2 ad. ♀♀. BIOGAS IV-DS55: 4 ad. ♂♂, 4 imm. ♂♂, 2 ad. ♀♀, 11 imm, ♀♀, 10 juv. Ch106-326: 13 ad. ♂♂, 4 imm. ♂♂, 26 ad. ♀♀, 6 imm. ♀♀, 7 juv.

DESCRIPTION. Adult female, length 4·6 mm: carapace (Fig. 34a, b) entirely smooth, pearly white, more than twice as long as deep, laterally somewhat compressed, without lateral laminar expansions; pseudorostrum moderately long; antero-lateral angle only a little produced, without a tooth or serrations behind it; eyelobe rudimentary. Gut coiled. Anterior 4 pereonites with dorsal projections; last pereonite and first two pleonites with dorsal teeth.

Antenna 1 (Fig. 34c) with first two segments of peduncle about equal in length and each about $1\frac{1}{2}$ as long as the third. Maxilliped 3 (Fig. 34d) with basis a little curved, not much longer than remaining segments together. Pereopod 1 (Fig. 34e) with basis nearly 2/3 as long as remaining segments together with a few teeth distally on its ventral edge; the ischium also has some ventral distal teeth; the merus is about twice as long as the ischium and less than

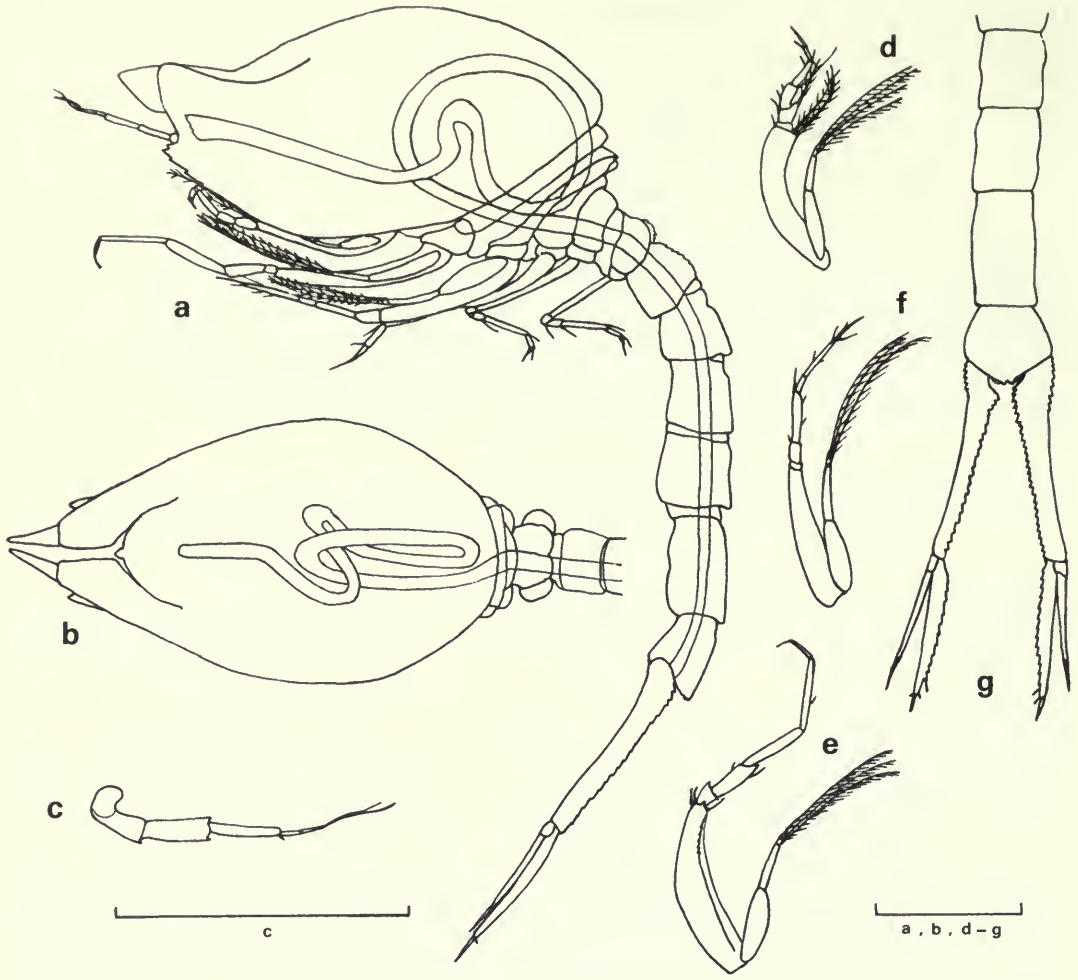

Fig. 33 *Platycuma hessleri* ♀, (a) lateral view; (b) carapace and pereon from above; (c) antenna 1; (d) maxilliped 3; (e) pereopod 1; (f) pereopod 2; (g) uropods and end of pleon.

2/3 as long as the carpus, which is a little longer than the propodus and twice as long as the dactyl. Pereopod 2 (Fig. 34f) with basis a little shorter than remaining segments together, the carpus very little longer than the dactyl and about three times as long as the propodus. Uropod (Fig. 34g) very little longer than the last two pleonites together, peduncle almost straight and with a few teeth near the base on the inner edge; the endopod is about 4/5 as long as the peduncle and has serrations and spines on its inner edge; the exopod is little more than 2/3 as long as the endopod.

Adult male. Generally similar to the female. The antero-lateral angle is marked by a spine. The second antennal flagellum is short.

TYPE LOCALITY. 50° 04.9′ N–50° 05.3′ N, 14° 23·8′ W–14° 24.8′ W, 3859 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 335 : 1, allotype 1982 : 336 : 1, paratypes 1982 : 337 : 10.

REMARKS. In appearance this species is similar to *Cumellopsis* from which it is distinguished only by the coiled gut. From *Platycuma hessleri,* which it generally resembles, it may be distinguished by the pearly white, almost iridescent, appearance of its carapace, which in the female is more than twice as long as deep but less than twice as long as deep in *P. hessleri.*

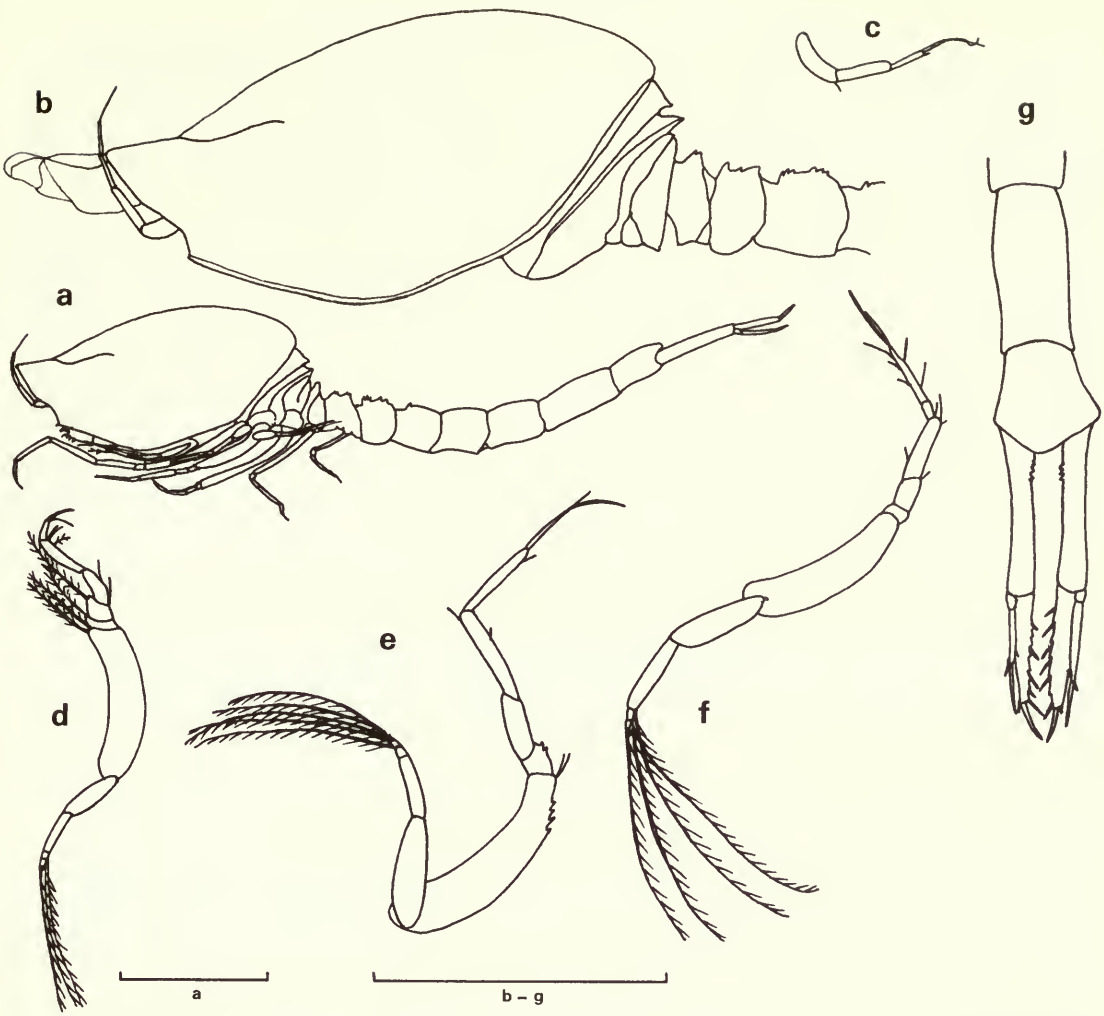

Fig. 34 *Platycuma candida* ♀, (a) lateral view; (b) carapace and pereon from side; (c) antenna 1; (d) maxilliped 3; (e) pereopod 1; (f) pereopod 2; (g) uropods and end of pleon.

DISTRIBUTION. Recorded so far at few stations west of Ireland and in the Bay of Biscay in rather deep water, between 3548 and 4226 m.

Genus ***PROCAMPYLASPIS*** Bonnier, 1896

Molar process of mandible styliform. Second maxillipeds with the dactyl shaped like a rake. First pereopod with the ischium long.

In this genus important distinguishing characters may be found in the armature of the carapace, the shape and armature of the eyelobe, the form of the dactyl in the second maxilliped and the relative proportions of the uropods. There is considerable sexual dimorphism in the adult stages and carapace armature and shape of males may differ from those of females.

Including the 8 new species described in this paper, there are now 21 species known in the genus.

Procampylaspis armata Bonnier, 1896

MATERIAL. MBAUK-29: 4 ad. ♀♀, 1 imm. ♀. 56: 3 ad. ♂♂, 3 imm. ♂♂, 15 ad. ♀♀, 14 juv. 65: 1 ad. ♂, 4 ad. ♀♀, 1 imm. ♀, 8 juv. IOS-6701: 1 ad. ♂, 6 ad. ♀♀. 6709: 2 imm. ♂♂, 1 ad. ♀, 1 juv. 6711: 1 ad. ♀. SMBA-ES4: 7 ad. ♂♂, 4 imm. ♂♂, 11 ad. ♀♀, 6 imm. ♀♀, 7 juv. ES12: 2 ad. ♂♂, 3 imm. ♂♂, 10 ad. ♀♀, 10 imm. ♀♀, 18 juv. *Thalassa* 70-W357: 7 ad. ♂♂, 12 ad. ♀♀, 5 imm. ♀♀, 40 juv. W371: 3 ad. ♂♂. *Thalassa* 72-Y374: 1 juv. *Thalassa* 73-Z399: 1 imm. ♀. Z416: 1 imm. ♀. Z428: 1 ad. ♂. Z434: 1 ad. ♂. Z440: 1 imm. ♀. Z443: 2 ad. ♂♂, 1 ad. ♀, 2 imm. ♀♀. BIOGAS I-DS05: 1 ad. ♀, 1 imm. ♀, 1 juv. DS09: 2 ad. ♂♂, 11 ad. ♀♀, 3 imm. ♀♀. DS11: 2 ad. ♀♀. DS12: 4 ad. ♀♀. DS13: 2 ad. ♂♂, 15 ad. ♀♀, 14 imm. ♀♀, 8 juv. POLYGAS-DS15: 3 ad. ♂♂, 5 imm. ♂♂, 44 ad. ♀♀, 54 imm. ♀♀. DS17: 2 imm. ♂♂, 5 ad. ♀♀, 2 juv. DS18: 4 ad. ♂♂, 8 imm. ♂♂, 22 ad. ♀♀, 34 imm. ♀♀. DS21: 3 imm. ♀♀. DS25: 4 ad. ♂♂, 3 imm. ♂♂, 10 ad. ♀♀, 2 imm. ♀♀, 5 juv. DS26: 6 ad. ♂♂, 18 ad. ♀♀, 13 imm. ♀♀. BIOGAS II-DS31: 4 ad. ♂♂, 1 imm. ♂, 5 ad. ♀♀, 3 imm. ♀♀. DS32: 1 ad. ♂, 3 imm. ♂♂, 8 ad. ♀♀, 1 imm. ♀. BIOGAS II-DS35: 5 ad. ♀♀, 7 imm. ♀♀. DS36: 8 ad. ♀♀, 2 imm. ♀♀. DS37: 5 ad. ♀♀, 2 juv. DS38: 1 imm. ♂, 2 ad. ♀♀, 4 imm. ♀♀. DS41: 5 ad. ♀♀. DS49: 1 imm. ♂, 3 ad. ♀♀, 4 imm. ♀♀, 1 juv. DS50: 3 ad. ♂♂, 7 imm. ♂♂, 6 ad. ♀♀, 8 imm. ♀♀, 1 juv. BIOGAS IV-DS51: 9 ad. ♂♂, 2 imm. ♂♂, 10 ad. ♀♀, 3 imm. ♀♀, 7 juv. DS52: 7 imm. ♂♂, 3 ad. ♀♀, 14 imm. ♀♀. DS62: 1 ad. ♂, 3 imm. ♂♂, 8 ad. ♀♀, 8 imm. ♀♀. DS63: 9 ad. ♀♀, 3 imm. ♀♀. DS64: 1 ad. ♂, 7 imm. ♀♀. BIOGAS VI-DS86: 12 ad. ♂♂, 7 imm. ♂♂, 9 ad. ♀♀, 11 imm. ♀♀, 1 juv. DS87: 4 ad. ♂♂, 3 imm. ♂♂, 24 ad. ♀♀, 7 imm. ♀♀, 13 juv. CP09: 4 ad. ♀♀, 9 imm. ♀♀, 8 juv. CP23: 1 imm. ♂, 6 imm. ♀♀, 17 juv. CP24: 2 ad. ♂♂, 1 imm. ♂. CP25: 3 imm. ♀♀. AII31-144: 1 ad. ♂. AII42-201: 1 ad. ♀, 1 imm. ♀, 3 juv. AII59-211: 22 ad. ♂♂, 105 ad. ♀♀, 4 juv. Kn25–295: 1 ad. ♂, 2 imm. ♂♂, 4 ad. ♀♀, 8 imm. ♀♀, 16 juv. 297: 3 ad. ♂♂, 6 imm. ♂♂, 16 ad. ♀♀, 23 imm. ♀♀.

DISTRIBUTION. Previously recorded from the north-east Atlantic and the Mediterranean, *P. armata* is now found to be widespread throughout the eastern part of the Atlantic both north and south of the equator and is also recorded from off Surinam. It occurs throughout a wide depth range, at least from 119 m to 4547 m, but mainly on the continental slope.

Procampylaspis bonnieri Calman, 1906

MATERIAL. SMBA-ES10: 22 ad. ♂♂, 13 imm. ♂♂, 46 ad. ♀♀, 18 imm. ♀♀, 35 juv. BIOGAS VI-DS76: 1 imm. ♂. AII31-156: 1 imm. ♂, 1 imm. ♀.

DISTRIBUTION. Found previously only in the Mediterranean between 950 and 1200 m and also between 466 and 2665 m (Reyss, 1972) it is now recorded from a few localities west of Scotland and in the Bay of Biscay as well as from the mid-Atlantic ridge betwen Dakar and Recife in depths down to 4228 m.

Procampylaspis bituberculata Hansen, 1920

MATERIAL. SMBA-ES18: 1 imm. ♀. ES20: 2 ad. ♂♂, 1 imm. ♂, 4 ad. ♀♀. *Thalassa* 72-Y374: 2 ad. ♀♀, 1 imm. ♀, 1 juv. *Thalassa* 73-Z400: 2 ad. ♀♀. Z429: 1 ad. ♂, 2 imm. ♂♂, 3 ad. ♀♀, 9 imm. ♀♀. Z442: 1 ad. ♀. Z451: 1 ad. ♀. BIOGAS I-DS14: 1 ad. ♂, 4 ad. ♀♀. BIOGAS II-DS33: 2 ad. ♂♂, 3 imm. ♂♂, 5 ad. ♀♀, 1 imm. ♀, 8 juv. DS34: 1 imm. ♂.

REMARKS. The male has less pronounced tubercles than the female. The female has relatively short uropod peduncles.

DISTRIBUTION. Previously recorded only from south-west of the Faroes in 847–941 m, it has now been found at several stations west of Scotland and in Biscay between 975 and 2338 m.

Procampylaspis macronyx Hansen, 1920

MATERIAL. MBAUK-44: 1 imm. ♂, 1 imm. ♀. SMBA-ES20: 6 ad. ♀♀, 1 imm. ♀. ES140: 1 imm. ♂, 1 imm. ♀. ES147: 2 ad. ♀♀. *Thalassa* 73-Z429: 1 ad. ♀, 1 juv. Z436: 1 imm. ♂. Z447: 2 ad. ♀♀. BIOGAS I-DS13: 1 imm. ♂. POLYGAS-DS15: 4 imm. ♀♀, 6 juv. DS16: 1 ad. ♀, 1 juv. DS18: 1 ad. ♂, 2 imm. ♂♂, 4 ad. ♀♀. BIOGAS VI-DS79: 1 imm. ♂. Ch106-321: 1 ad. ♂, 1 imm. ♂. 323: 1 ad. ♀.

DISTRIBUTION. Recorded by Hansen from two localities west of Iceland and south-west of the Faroes between 975 and 1441 m. It is now recorded from a number of stations west of Scotland and in Biscay down to 4715 m in greater numbers than *P. bituberculata.*

Procampylaspis arguini Bacescu and Muradian, 1972

MATERIAL. SMBA-ES18: 1 ad. ♂, 8 imm. ♂♂, 1 imm. ♀, 2 juv. AII42-189: 8 ad. ♂♂, 18 ad. ♀♀. 192: 5 ad. ♀♀. 200: 1 imm. ♂, 1 ad. ♀, 1 juv. 201: 1 ad. ♀, 1 juv.

DISTRIBUTION. Originally found off the coast of Morocco in only 22 m, it is now recorded in greater depths off the west of Scotland and south-west Africa between 1014 and 2754 m.

Procampylaspis thalassae Bacescu and Muradian, 1972

MATERIAL. IOS-6697: 1 ad. ♂. AII42-202: 1 imm. ♂, 1 juv.

DISTRIBUTION. Also recorded from the Moroccan coast in 227–286 m, it is now recorded at a station off the Canary Islands in 1564 m and another off south-west Africa in 1643 m.

Procampylaspis inermis sp. nov.
(Fig. 35)

MATERIAL. SMBA-ES20: 2 ad. ♂♂, 2 imm. ♂♂, 9 ad. ♀♀, 4 imm. ♀♀, 1 juv. *Thalassa* 73-Z425: 1 ad. ♂. POLYGAS-DS20: 4 imm. ♂♂, 2 ad. ♀♀. AII12-70: 3 ad. ♂♂, 3 imm. ♂♂, 11 ad. ♀♀. 73: 24 ad. ♂♂, 3 imm. ♂♂, 46 ad. ♀♀, 25 imm. ♀♀. Ch58-103: 5 ad. ♂♂, 8 imm. ♂♂, 31 ad. ♀♀, 1 imm. ♀. AII24-125: 1 ad. ♀. AII30-131: 4 ad. ♂♂, 9 imm. ♂♂, 24 ad. ♀♀, 1 imm. ♀, 1 juv. AII31-142: 2 ad. ♂♂, 10 ad. ♀♀, 2 imm. ♀♀. Ch88-209: 1 imm. ♂, 1 imm. ♀. Kn25-293: 22 ad. ♂♂, 19 imm. ♂♂, 170 ad. ♀♀, 15 imm. ♀♀. 299: 2 ad. ♂♂, 3 ad. ♀♀, 2 imm. ♀♀. 301: 5 ad. ♂♂, 22 ad. ♀♀, 5 imm. ♀♀. 303: 4 ad. ♂♂, 4 ad. ♀♀, 5 imm. ♀♀. Ch106–318: 1 imm. ♀. 321: 1 ad. ♂, 2 ad. ♀♀.

DESCRIPTION. Ovigerous female, length 3·1 mm: carapace (Fig. 35a, b) smooth except for fairly long scattered setae, without spines, 1 2/3 as long as deep; pseudorostrum truncate anteriorly, a little more than 1/6 of the total carapace length, siphons short; antero-lateral angle little produced, marked by a small spine; eyelobe pointed, less than 1/3 as long as pseudorostrum, longer than the breadth at its base. Pereon and pleon somites without spines or other projections apart from a few setae.

Antenna 1 (Fig. 35e) with basal segment slender, a little longer than the subequal second and third. Maxilliped 2 (Fig. 35f, g) with dactylar projections rather narrow, the basal one bifid followed by two longer more distal projections with a short one between them. Maxilliped 3 (Fig. 35h) with basis narrow, somewhat curved, a little projecting distally, nearly as long as remaining segments together; merus long but not much expanded, nearly as long as subequal carpus and propodus together; propodus about twice as long as dactyl. Pereopod 1 (Fig. 35i) with basis narrow distally, little more than half as long as remaining segments together. Pereopod 2 (Fig. 35j) with basis somewhat more than half as long as remaining segments together; dactyl about as long as merus and carpus together and more than three times as long as propodus; the carpus is broadened distally and has a spine on its lower distal point. Uropod (Fig. 35k) slender, with peduncle distinctly longer than last two pleonites together and nearly 1½ as long as the endopod which is much longer than the exopod; the peduncle has a few setae along either side and the endopod about three spines on its inner edge and a robust terminal spine; the terminal spine of the exopod is long and slender and reaches about as far as the terminal spine of the endopod.

Adult male, length 3·0 mm: carapace (Fig. 35c, d) less arched dorsally and narrower than in adult female and showing a marked hexagonal reticulate pattern; the antero-lateral angles are more prominent. In other respects it has the usual differences from the female.

TYPE LOCALITY. 8° 28.8′ N, 56° 04.5′ W, 2842–2853 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 338 : 1, allotype 1982 : 339 : 1, paratypes 1982 : 340 : 10.

REMARKS. *P. inermis* is characterized by its lack of armature apart from setae on the carapace and by the eyelobe which although without lenses is of normal shape, neither small or elongated.

DISTRIBUTION. Found on either side of the Atlantic from the tropical region northwards between 700 and 4825 m depth.

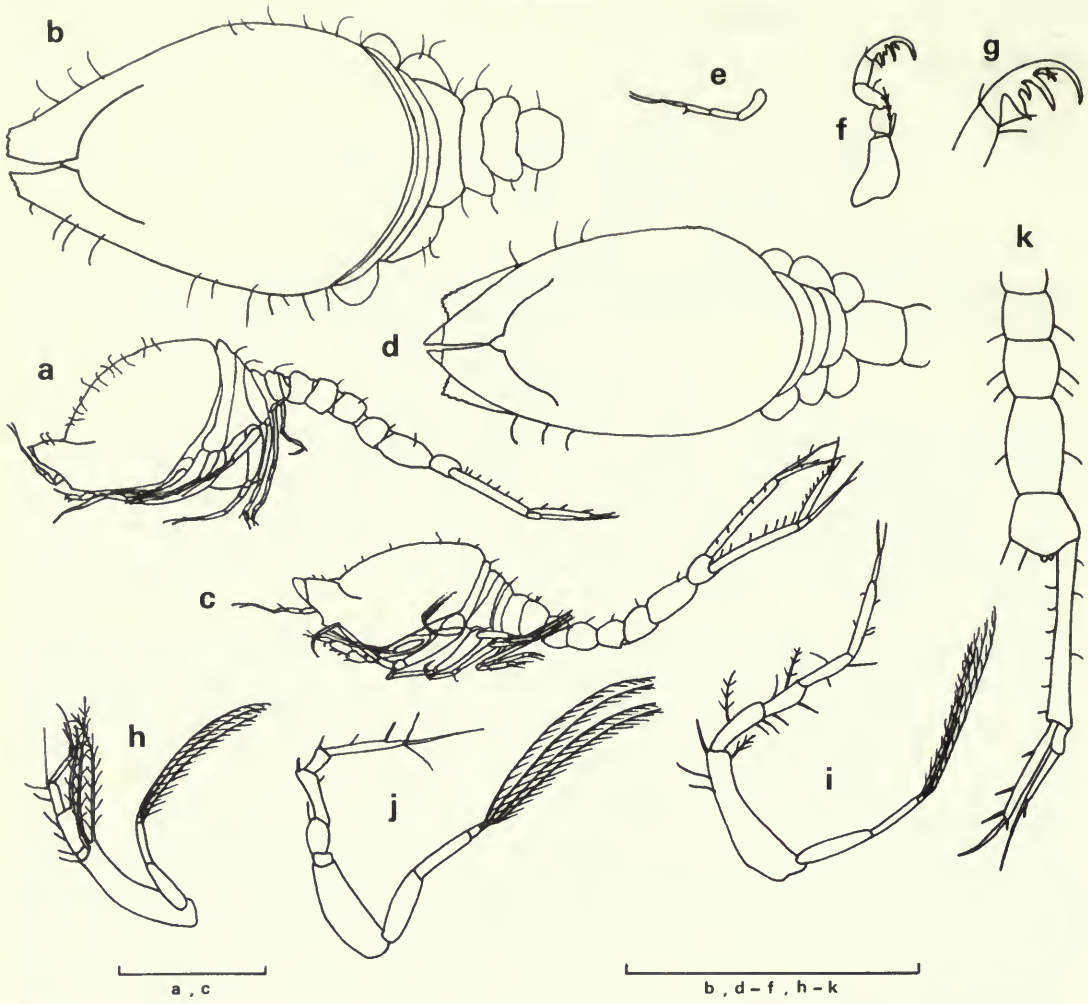

Fig. 35 *Procampylaspis inermis,* (a) ovigerous ♀ from side; (b) ♀ carapace and pereon from above; (c) adult ♂ from side; (d) ♂ carapace and pereon from above; (e) ♀ antenna 1; (f) maxilliped 2; (g) distal part of maxilliped 2 (further enlarged); (h) maxilliped 3; (i) pereopod 1; (j) pereopod 2; (k) uropod and end of pleon.

Procampylaspis procurrens sp. nov.
(Fig. 36)

MATERIAL. AII42-195: 3 imm. ♀♀, 1 juv. AII60-239: 1 ad. ♀. 240: 16 ad. ♂♂, 9 imm. ♂♂, 47 ad. ♀♀, 27 imm. ♀♀, 8 juv. 245: 7 ad. ♂♂, 8 ad. ♀♀, 6 imm. ♀♀. 262: 3 ad. ♂♂, 6 imm. ♂♂, 22 ad. ♀♀, 32 imm. ♀♀. 264: 2 juv.

DESCRIPTION. Adult female, length 3·9 mm: carapace (Fig. 36a, b) raised dorsally, more than 1½ as long as deep, with a single fairly prominent forward-pointing mid-dorsal spine and few scattered setae; antero-lateral angle distinct but blunt; the eyelobe is fairly but not very narrow and reaches forward to about 2/3 as far as the pseudorostrum, ending in a forward-pointing spine, which may occasionally have a smaller spine behind it; the pseudorostrum is abruptly truncate in front. The first two pereon somites are produced dorsally into bifid lappets and the last two have small dorsal spines. The pleon somites are usually without spines or projections but there are sometimes a few blunt spines dorso-laterally on pleonite 5.

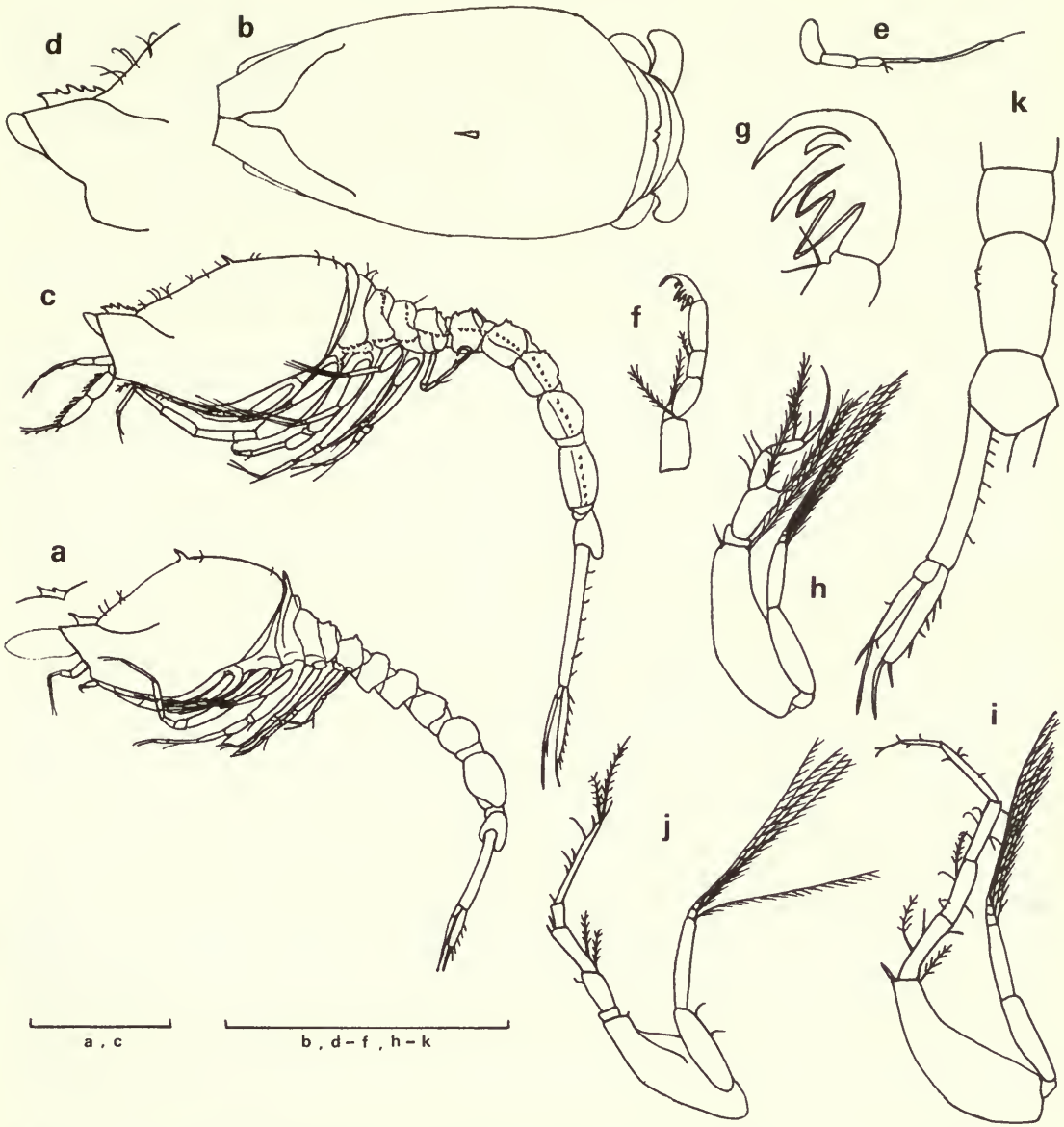

Fig. 36 *Procampylaspis procurrens,* (a) adult ♀ from side; (b) ♀ carapace and pereon from above; (c) adult ♂ from side; (d) adult ♂ front of carapace from side; (e) ♀ antenna 1; (f) maxilliped 2; (g) distal part of maxilliped 2 (further enlarged); (h) maxilliped 3; (i) pereopod 1; (j) pereopod 2; (k) uropod and end of pleon.

Antenna 1 (Fig. 36e) has the three peduncle segments diminishing in length distally, the basal segment fairly robust. Maxilliped 2 (Fig. 36f, g) with dactylar spines rather broad, the basal unequally bifid and the most distal not noticeably longer than the medial spines. Maxilliped 3 (Fig. 36h) with basis about as long as remaining segments together, the merus broadened distally. Pereopod 1 (Fig. 36i) with basis broad at base, little more than half as long as remaining segments together, with a prominent distal spine; the ischium is slender and longer than the merus. Pereopod 2 (Fig. 36j) with basis about $\frac{3}{4}$ as long as remaining segments together, the carpus with two distal spines, the dactyl slender and much longer

than the carpus and propodus together. Uropod (Fig. 36k) with basis distinctly shorter than last two pleon somites together, about 1½ as long as the endopod, which is fairly broad and not much longer than the exopod; the peduncle has a few setae on its inner edge and the endopod some slender spines but there are no pronounced serrations.

Adult male, length 4·6 mm. Differing from female in usual characters but additionally the carapace (Fig. 36c) is less arched and the eyelobe (Fig. 36d) has about 5 teeth in a single row mid-dorsally, there are more projections on the pereon and pleon somites, especially in a dorso-lateral row on either side, and the uropod is longer and more slender.

TYPE LOCALITY. 36° 55.7′ S, 53° 01.4′ W, 2702 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 341 : 1, allotype 1982 : 342 : 1, paratypes 1982 : 343 : 10.

REMARKS. *P. procurrens* may be distinguished by the single procurved mid-dorsal spine on the carapace in either sex and by the eyelobe which is elongated but not narrow, ending in a strong spine, and with a single row of spines or serrations behind this in the male; there may be a further spine or tooth behind the end spine in the female. From *P. acanthomma* sp. nov. which it somewhat resembles it is further distinguished by the relative shortness of the terminal spine on the dactyl of the second maxilliped.

DISTRIBUTION. Found at present on either side of the South Atlantic, from off South-west Africa and the Argentine in depths between 1679 and 3797 m.

Procampylaspis lutensis sp. nov.
(Fig. 37)

MATERIAL. IOS-6696: 2 juv. 6697: 1 ad. ♂, 1 imm. ♂. 6701: 2 ad. ♂♂, 1 ad. ♀. 6714: 1 ad. ♀. SMBA-ES18: 4 ad. ♂♂, 3 imm. ♂♂, 21 ad. ♀♀, 3 imm. ♀♀. *Thalassa* 73-Z421: 1 ad. ♀, 1 imm. ♀, Z422: 1 imm. ♀. Z428: 2 imm. ♀♀. Z435: 1 ad. ♀. Z438: 1 ad. ♂, 1 ad. ♀. 2445: 1 ad. ♂, 2 ad. ♀♀, 1 imm. ♀. Z453: 1 imm. ♂, 2 ad. ♀♀, 1 imm. ♀. BIOGAS I-DS05: 6 ad. ♂♂, 2 imm. ♂♂, 8 ad. ♀♀, 7 juv. DS06: 4 ad. ♀♀, 3 imm. ♀♀. DS07. 1 ad. ♂, 1 ad. ♀. DS08: 1 ad. ♀. DS11: 3 imm. ♂♂, 8 ad. ♀♀. DS13: 2 ad. ♂♂, 7 ad. ♀♀, 2 imm. ♀♀. DS14: 2 ad. ♂♂. POLYGAS-DS15: 6 ad. ♂♂, 7 imm. ♂♂, 24 ad. ♀♀, 3 imm. ♀♀. DS17: 2 ad. ♂♂, 1 imm. ♂, 2 ad. ♀♀, 1 imm. ♀. DS18: 14 ad. ♂♂, 15 imm. ♂♂, 34 ad. ♀♀, 2 imm. ♀♀. DS25: 5 ad. ♂♂, 7 ad. ♀♀, 2 juv. DS26: 1 ad. ♂, 2 ad. ♀♀. BIOGAS II-DS32: 1 ad. ♀. BIOGAS III-DS35: 3 imm. ♂♂, 3 ad. ♀♀. DS36: 2 imm. ♂♂, 2 ad. ♀♀, 3 imm. ♀♀. DS37: 3 ad. ♂♂, 3 ad. ♀♀. DS50: 1 ad. ♂, 1 imm. ♂. BIOGAS IV-DS51: 1 ad. ♂, 1 imm. ♂, 5 ad. ♀♀, 4 imm. ♀♀, 5 juv. DS52: 2 ad. ♂♂, 1 imm. ♂, 4 ad. ♀♀, 6 imm. ♀♀. DS55: 1 imm. ♂, 5 ad. ♀♀, 4 imm. ♀♀. DS62: 1 ad. ♀. DS63: 2 ad. ♂♂, 1 imm. ♂, 1 ad. ♀. DS64: 10 ad. ♂♂, 1 imm. ♂, 7 ad. ♀♀, 1 imm. ♀. BIOGAS V-DS66: 2 ad. ♂♂, 5 ad. ♀♀. DS67: 2 ad. ♂♂, 1 imm. ♂, 2 imm. ♀♀. BIOGAS VI-DS86: 3 ad. ♂♂, 9 imm. ♂♂, 7 ad. ♀♀, 14 imm. ♀♀, 5 juv. DS87: 14 ad. ♂♂, 5 ad. ♀♀, 11 imm. ♀♀, 8 juv. DS88: 1 ad. ♀, 1 juv. CP09: 2 ad. ♀♀, 4 imm. ♀♀. CP23: 3 ad. ♂♂, 7 imm. ♂♂, 3 ad. ♀♀, 5 imm. ♀♀, 4 juv. CP24: 2 ad. ♂♂, 5 imm. ♀♀. CP25: 7 ad. ♂♂, 3 imm. ♂♂, 9 ad. ♀♀, 4 imm. ♀♀, 8 juv. AII31-142: 4 ad. ♂♂, 1 imm. ♂, 4 ad. ♀♀, 3 imm. ♀♀.

DESCRIPTION. Adult female, length 2·8 mm: carapace (Fig. 37a-c) not much elevated dorsally, almost twice as long as deep, usually but not always with a small mid-dorsal spine; pseudorostrum abruptly truncated in front, siphons fairly long; eyelobe narrow, not elongated, reaching less than half way to the tip of the pseudorostrum, upstanding in front, ending in a small forward-pointing spine; antero-lateral angle only slightly prominent. Anterior pereon somites with bifid dorsal lappets but posterior pereonites and pleon somites without projections.

Antenna 1 (Fig. 37d) with basal segment curved, fairly slender, about 1½ as long as subequal second or third segments. Maxilliped 2 (Fig. 37e-f) with most distal dactylar spine distinctly longer than the others. Maxilliped 3 (Fig. 37g) with basis nearly as long as remaining segments together, the merus slender but wider distally, about 1½ as long as the carpus, which is about as long as the propodus and longer than the dactyl. Pereopod 1 (Fig. 37h) with basis about 2/3 as long as remaining segments together; the propodus is about twice as long as the dactyl and slightly longer than the merus which is itself a little longer than the subequal

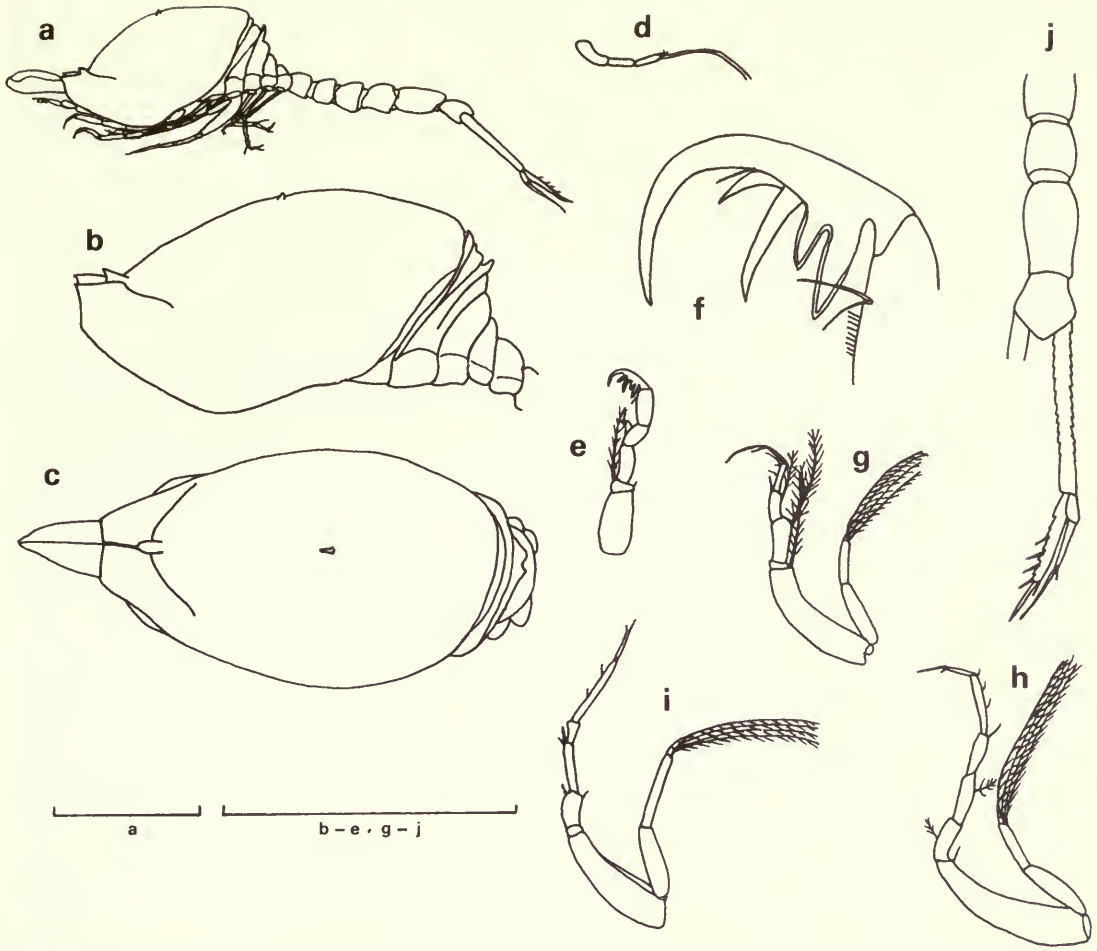

Fig. 37 *Procampylaspis lutensis* ♀, (a) lateral view; (b) carapace and pereon from side; (c) carapace and pereon from above; (d) antenna 1; (e) maxilliped 2; (f) distal part of maxilliped 2 (further enlarged); (g) maxilliped 3; (h) pereopod 1; (i) pereopod 2; (j) uropod and end of pleon.

ischium or carpus. Pereopod 2 (Fig. 37i) with basis less than 2/3 as long as remaining segments together; the relative proportions of the other segments much as in *P. inermis*. Uropods (Fig. 37j) with peduncle a little longer than the last two pleonites together and nearly twice as long as the endopod, which is about $1\frac{1}{3}$ as long as the exopod; the peduncle is serrated on the inner and outer edges and the endopod on its inner edge where there are also about 4 slender spines.

Adult male differs from female in usual respects.

TYPE LOCALITY. 56° 44′ N, 09° 20′ W, 1392–1450 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 344 : 1, allotype 1982 : 345 : 1, paratypes 1982 : 346 : 10.

REMARKS. In *P. lutensis* the eyelobe, although a little elongated and ending in a short spine, is less than half as long as the pseudorostral lobes. There is a single short mid-dorsal spine on the carapace which lacks other spines or setae.

DISTRIBUTION. Recorded in some quantity from the eastern side of the Atlantic from tropics northwards, between 720 and 4150 m depth.

Procampylaspis acanthomma sp. nov.
(Fig. 38)

MATERIAL. AII31-155: 2 ad. ♂♂, 1 ad. ♀. 156: 5 ad. ♂♂, 5 imm. ♂♂, 22 ad. ♀♀, 4 imm. ♀♀. 159: 3 imm. ♀♀, 3 juv. 167: 2 ad. ♂♂, 4 imm. ♂♂, 2 ad. ♀♀, 1 imm. ♀. 169: 2 ad. ♂♂, 5 imm. ♂♂, 12 ad. ♀♀, 5 imm. ♀♀. Kn25-291: 1 ad. ♂, 1 ad. ♀, 2 imm. ♀♀, 1 juv. 306: 2 imm. ♂♂, 3 imm. ♀♀, 1 juv. Ch106-321: 4 ad. ♂♂, 22 ad. ♀♀, 5 imm. ♀♀, 1 juv. 323: 3 ad. ♂♂, 2 ad. ♀♀, 1 juv. 326: 1 imm. ♀.

DESCRIPTION. Adult female, length 3·7 mm: carapace (Fig. 38a-c) without spines but with slight dorsal serrations and scattered setae, about $1\frac{3}{4}$ as long as deep, its integument covered with small irregular hexagonal reticulations; the pseudorostrum is fairly long, abruptly truncated in front, less than 1/6 of total carapace length, with a shallow but distinct antennal notch defined below by a rounded antero-lateral angle; the siphons are not very long; the eyelobe is fairly long and narrow in front, reaching a little beyond the middle of the pseudorostrum and ending in front with a prominent spine. The pereon and pleon somites are without spines but there are some setae on the pereon and faint serrations on the pleon; the first two pereonites have bifid lappets dorsally.

Antenna 1 (Fig. 39f) with basal segment fairly stout, curved, about $1\frac{1}{2}$ as long as the much longer than the third. Maxilliped 2 (Fig. 38f, g) with shorter part of bifid basal spine of dactyl much less than half as long as longer part; most distal spine somewhat longer than others. Maxilliped 3 (Fig. 38h) with basis a little shorter than remaining segments together, a little produced at its upper distal extremity and with some serrations or blunt spines distally below; the ischium has a spine on its lower edge; the merus is narrow and slightly shorter than the carpus. Pereopod 1 (Fig. 38i) with basis about 2/3 as long as remaining segments together; the propodus is distinctly longer than the carpus and three times as long as the dactyl. Pereopod 2 (Fig. 38j) with basis little more than half as long as remaining segments together; the relative lengths of these are much as in *P. lutensis,* except that of the dactyl, which is nearly as long as the merus and carpus combined. Uropods (Fig. 38k) with peduncle moderately long, distinctly longer than last two pleonites together and a little more than $1\frac{1}{2}$ as long as the endopod, which is less than $1\frac{1}{2}$ as long as the exopod; the peduncle is smooth with a few short setae and the endopod has a few slender spines on its inner edge.

Adult male (Fig. 38d) showing usual differences from female but also with many short spines dorsally and on the sides posteriorly on the carapace. There are spines dorsally and laterally on the pereon and at the sides of the pleon somites.

TYPE LOCALITY. 00° 46′ S-00° 46.5′ S, 29° 28′ W–29° 24′ W, 3459 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 347 : 1, allotype 1982 : 348 : 1, paratypes 1982 : 349 : 10.

REMARKS. The lack of carapace spines in the female, on which there are only a few low serrations and some setae, together with the fairly elongate eyelobe ending in a prominent spine, distinguishes this species. The adult male is characterised by the fairly large number of small spines dorsally and on the pereon.

DISTRIBUTION. Found on a few occasions off Brazil in the tropical Atlantic and off Surinam and west of Ireland in the North Atlantic between 587 and 3868 m.

Procampylaspis serratoculus sp. nov.
(Fig. 39)

MATERIAL. AII31-169: 3 ad. ♂♂, 10 imm. ♂♂, 27 ad. ♀♀, 4 imm. ♀♀. Kn25-295: 8 ad. ♂♂, 9 imm. ♂♂, 34 ad. ♀♀, 34 imm. ♀♀.

DESCRIPTION. Adult female, length 4·3 mm: carapace (Fig. 39a-c) less than twice as long as deep, integument with regular small hexagonal reticulations and with some spines in pairs or rows dorso-laterally; the pseudorostrum is about 1/7 of the total carapace length, abruptly truncate in front with fairly long siphons; the antennal notch is hardly defined and the antero-lateral angle is not at all prominent but is followed by a few small serrations; on either

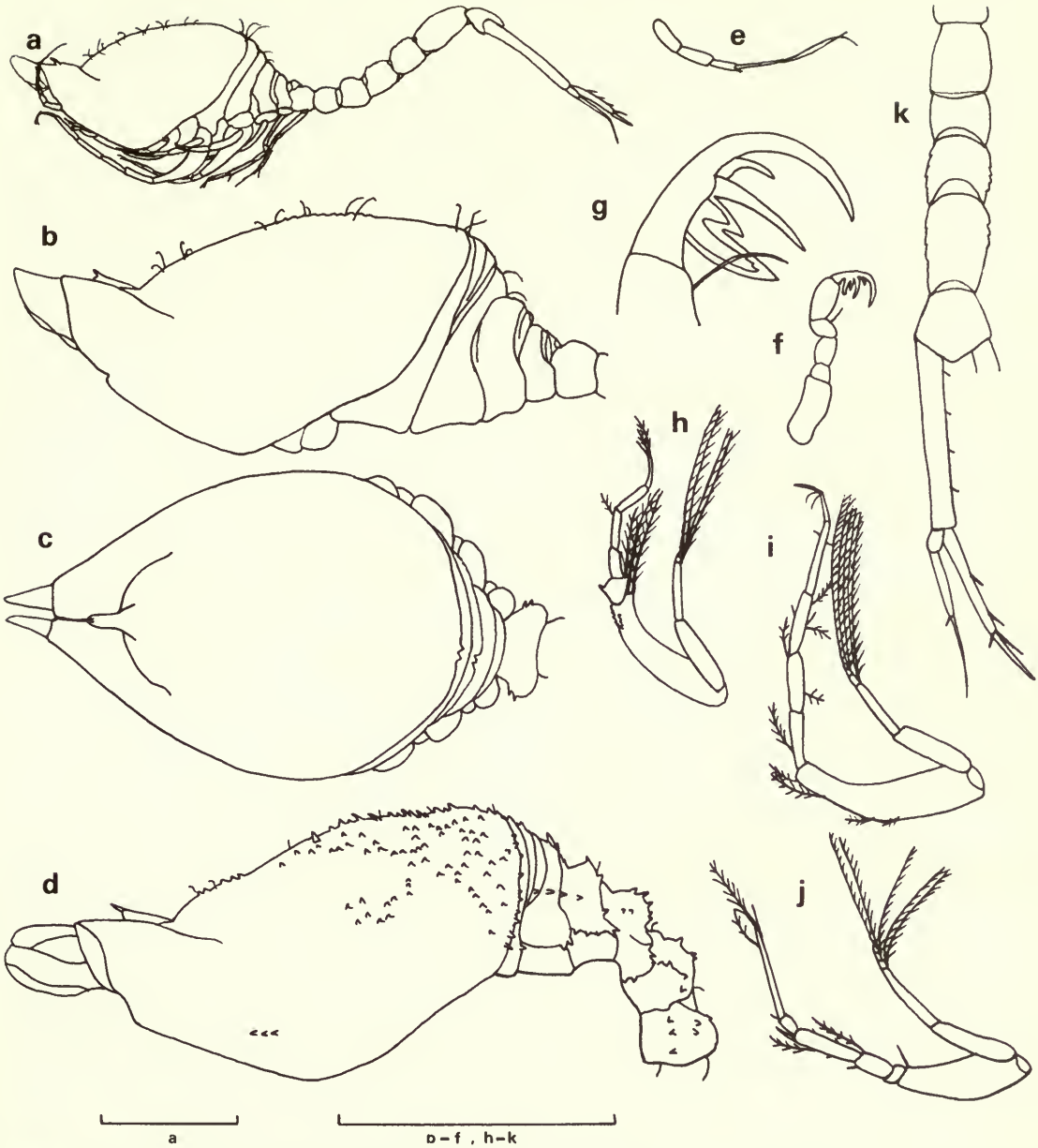

Fig. 38 *Procampylaspis acanthomma,* (a) adult ♀ from side ; (b) ♀ carapace and pereon from side; (c) ♀ carapace and pereon from above; (d) adult ♂ carapace and pereon from side; (e) ♀ antenna 1; (f) maxilliped 2; (g) distal part of maxilliped 2 (further enlarged); (h) maxilliped 3; (i) pereopod 1; (j) pereopod 2; (k) uropod and end of pleon.

side, a little set in from the edge is a fairly prominent spine; the eyelobe reaches about half way towards the front of the pseudorostrum; it is wider towards the front where there is a pair of spines followed by usually four in each of two rows diminishing in size towards the hind end. The anterior pereon somites are without spines but the first two have well defined paired dorsal lappets at their hind ends (Fig. 39d). There are a few small spines dorsally on the posterior pereon and pleon somites and the last two pleonites have some lateral spines.

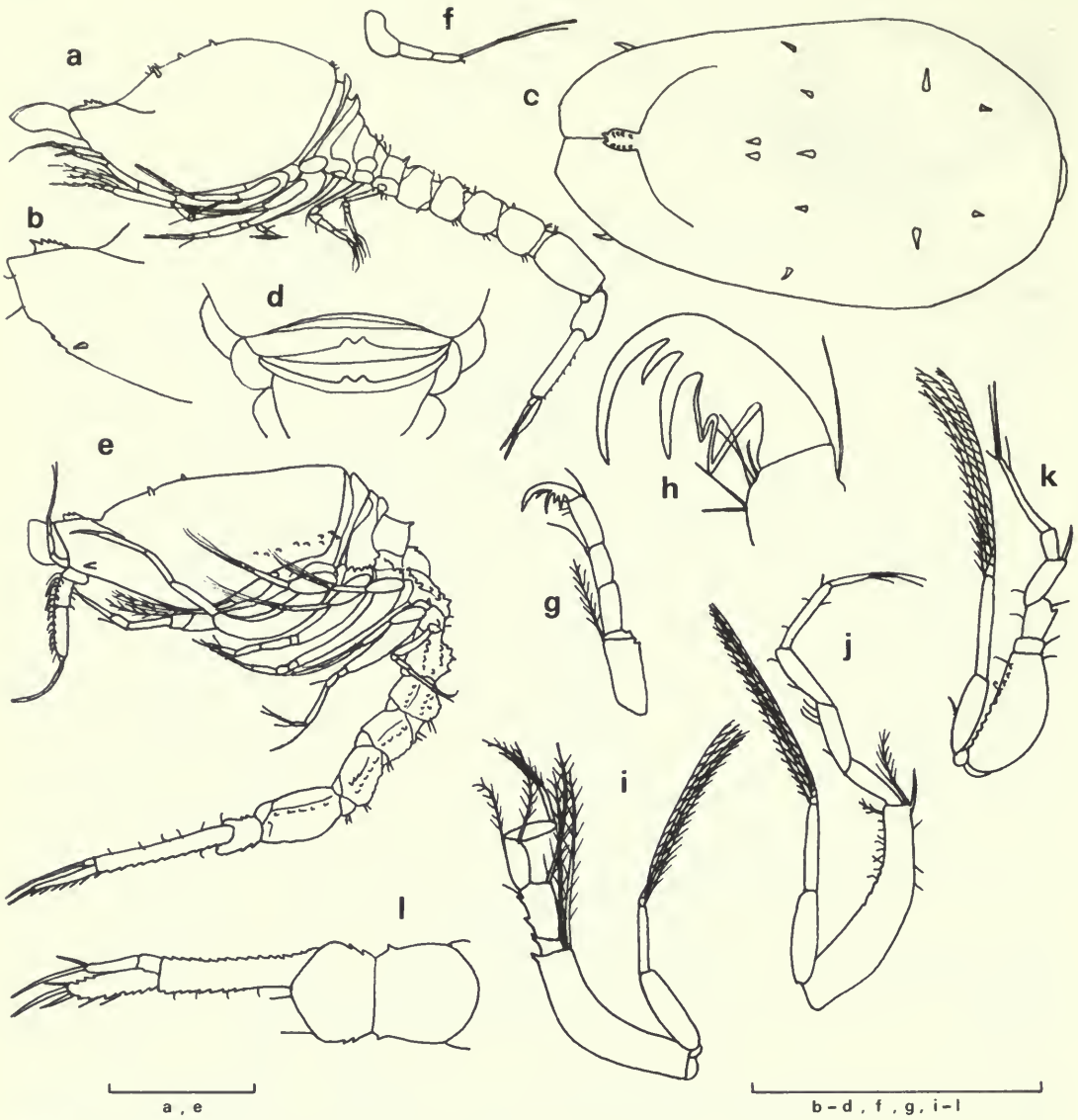

Fig. 39 *Procampylaspis serratoculus,* (a) adult ♀ from side; (b) ♀ front of carapace from side; (c) ♀ carapace from above; (d) ♀ hind end of carapace and pereon from above; (e) adult ♂ from side; (f) ♀ antenna 1; (g) maxilliped 2; (h) distal part of maxilliped 2 (further enlarged); (i) maxilliped 3; (j) pereopod 1; (k) pereopod 2; (l) uropod and end of pleon.

Antenna 1 (Fig. 39f) with basal segment fairly stout, curved, about $1\frac{1}{2}$ as long as the second segment which is longer than the third. Maxilliped 2 (Fig. 39g, h) with most distal dactylar spine rather longer than the remainder, the basal spine bifid. Maxilliped 3 (Fig. 39i) with basis curved, a little shorter than remaining segments together, with a small spine at its distal lower edge, the merus expanded distally above and with two blunt spines or serrations below; the merus is only slightly longer than the carpus, the propodus and dactyl being successively somewhat shorter. Pereopod 1 (Fig. 39j) with basis about 2/3 as long as remaining segments together, with a long distal spine on its lower edge and some serrations above; the ischium, merus and carpus are about equal in length and each distinctly shorter

than the propodus which is almost twice as long as the dactyl. Pereopod 2 (Fig. 39k) with basis stout, having a row of blunt spines along its upper edge; there is a short spine on the lower edge of the merus and a longer spine at the lower distal end of the carpus; the dactyl is long and a little curved, nearly three times as long as the propodus and $1\frac{1}{2}$ as long as the carpus. Uropod (Fig. 391) with peduncle rather short, serrated along both edges, shorter than the last two pleonites together and less than twice as long as the endopod; this has serrations on either edge and about three spines on the inner edge, with a long terminal spine; the exopod is serrated along the inner edge and is more than $\frac{3}{4}$ as long as the endopod.

Adult male, length 5·3 mm (Fig. 39e) differs in usual characters from female and has an irregular row of spines ventro-laterally on the hinder part of the carapace. There are many more spines laterally on the pereon somites and especially in rows at the sides of the pleon.

TYPE LOCALITY. 08° 03′ S–08° 02′ S, 34° 23′ W–34° 25′ W, 587 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 350 : 1, allotype 1982 : 351 : 1, paratypes 1982 : 352 : 10.

REMARKS. *P. serratoculus* is easily distinguished from other known species in the genus by the double row of spines or teeth on the prominent eyelobe. Although *P. procurrens* has several teeth on the eyelobe in the adult male these are in a single row.

DISTRIBUTION. Recorded at present from two stations only off the coasts of Brazil in 587 m and Surinam at 1000 m.

Procampylaspis ommidion sp. nov.
(Fig. 40)

MATERIAL. IOS-6697: 2 ad. ♀♀. 6701: 2 imm. ♀♀. SMBA-ES12: 2 ad. ♂♂, 3 imm. ♂♂, 2 ad. ♀♀, 5 imm. ♀♀. ES15: 2 ad. ♂♂, 1 imm. ♂, 14 ad. ♀♀, 4 imm. ♀♀, 16 juv. ES18: 2 imm. ♀♀. ES22: 2 ad. ♂♂, 3 imm. ♂♂, 9 ad. ♀♀, 9 imm. ♀♀, 4 juv. *Thalassa* 73-Z426: 9 imm. ♀♀. Z447: 3 imm. ♂♂. Z459: 2 imm. ♂♂, 7 imm. ♀♀. POLYGAS-DS15: 3 imm. ♂♂, 1 ad. ♀. DS16: 1 imm. ♂, 1 imm. ♀. DS18: 1 ad. ♀, 1 juv. BIOGAS III-DS41: 1 ad. ♂, 2 imm. ♂♂, 19 ad. ♀♀, 1 imm. ♀. BIOGAS VI-DS74: 1 ad. ♂, 2 imm. ♂♂, 1 ad. ♀. *Atlantis* 248-G # 9: 1 ad. ♂, 1 ad. ♀. AII12-61: 1 juv. Ch50-84: 7 imm. ♂♂, 4 ad. ♀♀. 85: 1 ad. ♂, 2 imm. ♂♂, 5 ad. ♀♀. AII23-106: 1 ad. ♂. AII24-118: 1 ad. ♂, 7 ad. ♀♀, 2 imm. ♀♀. 119: 2 ad. ♀♀. AII31-155: 1 ad. ♂, 1 imm. ♂, 5 ad. ♀♀, 2 imm. ♀♀. Ch106-334: 3 ad. ♂♂, 5 imm. ♂♂, 33 ad. ♀♀, 28 imm. ♀♀, 17 juv.

DESCRIPTION. Ovigerous female, length 4·7 mm: carapace (Fig. 40a, b) about twice as long as deep, less than $1\frac{1}{2}$ as long as broad, broader posteriorly, with a single mid-dorsal blunt spine or prominence and some short setae; the integument shows a faint reticulate pattern; pseudorostrum about $\frac{1}{6}$ of total carapace length, truncated in front but not abruptly, with some slight serrations anteriorly; the siphons are fairly long; the antero-lateral angle is scarcely apparent but there are some serrations behind it; the eyelobe is small but sharply pointed in front. The anterior pereonites have dorsal bifid lappets but otherwise pereon and pleon somites have only a few short setae.

Antenna 1 (Fig. 40c) with basal segment little curved, about as long as the second and third combined. Maxilliped 2 (Fig. 40d, e) comparatively stout; merus with some blunt distal spines; propodus with a lobed hyaline membrane along the inner edge; basal spine on dactyl bifid and most distal spine longer than others but not projecting much farther inwards. Maxilliped 3 (Fig. 40f) with basis a little shorter than remaining segments together, somewhat produced at its distal upper end; merus long, broadened distally, as long as carpus and propodus together; carpus with several fragile spines on upper edge. Pereopod 1 (Fig. 40g) with basis scarcely more than half as long as remaining segments together; ischium slender, longer than merus or propodus, each of which is longer than the carpus and twice as long as the slender dactyl. Pereopod 2 (Fig. 40h) with basis broad at base, about $\frac{3}{5}$ as long as remaining segments together; carpus with a long distal spine, about twice as long as merus but distinctly shorter than the dactyl. Uropod (Fig. 40i) with peduncle long and slender, without serrations but a few setae on its inner edge, nearly as long as last four pleonites

Fig. 40 *Procampylaspis ommidion* ovigerous ♀, (a) lateral view; (b) carapace from above; (c) antenna 1; (d) maxilliped 2; (e) distal part of maxilliped 2 (further enlarged); (f) maxilliped 3; (g) pereopod 1; (h) pereopod 2; (i) uropod and end of pleon.

together and more than twice as long as the endopod which has three slender spines on its inner edge and a strong terminal spine; the exopod is $\frac{3}{4}$ as long as the endopod.

Adult male with usual differences from female, without additional spines.

TYPE LOCALITY. 56° 44′ N, 09° 28′ W, 1632–1692 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 353 : 1, allotype 1982 : 354 : 1, paratypes 1982 : 355 : 10.

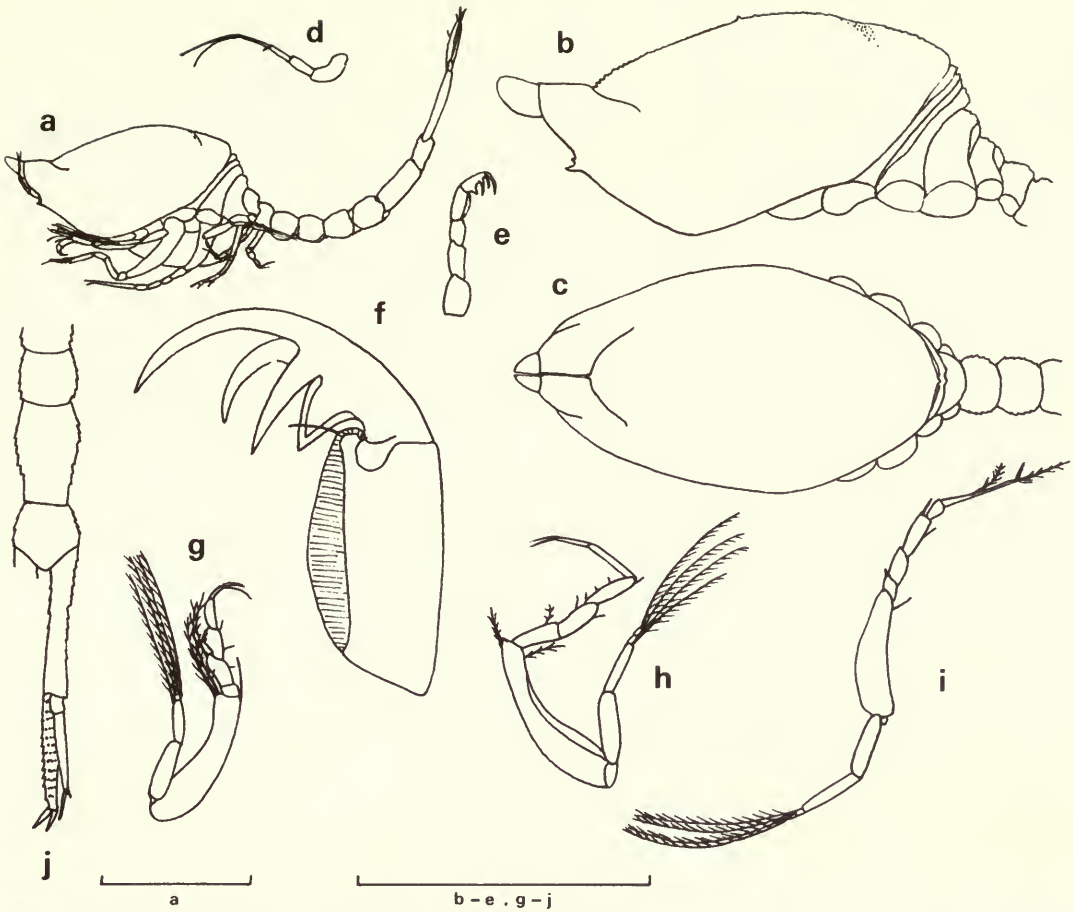

Fig. 41 *Procampylaspis profunda* ♀, (a) lateral view; (b) carapace and pereon from side; (c) carapace and pereon from above; (d) antenna 1; (e) maxilliped 2; (f) distal part of maxilliped 2 (further enlarged); (g) maxilliped 3; (h) pereopod 1; (i) pereopod 2; (j) uropod and end of pleon.

REMARKS. *P. ommidion* shows considerable resemblance to *P. bonnieri,* having similarly a reduced eyelobe, but the female has a low mid-dorsal tubercle on the carapace while the adult male has no additional spines on the carapace and pereon. The uropod peduncles are relatively longer than in *P. bonnieri* and there are some differences in the armature of the appendages.

DISTRIBUTION. Found in some quantity on both sides of the North Atlantic between 860 and 4749 m depth.

Procampylaspis profunda sp. nov.
(Fig. 41)

MATERIAL. AII31-156: 5 ad. ♂♂, 17 ad. ♀♀, 16 imm. ♀♀, 1 juv. AII40-175: 1 ad. ♀, 2 imm. ♀♀. AII42-192: 2 ad. ♂♂, 26 ad. ♀♀. 194: 1 imm. ♂, 1 imm. ♀. 202: 2 juv.

DESCRIPTION. Adult female, length 3·0 mm: carapace (Fig. 41a-c) almost twice as long as deep or as broad; pseudorostrum less than $\frac{1}{7}$ of total carapace length, abruptly truncated in front; siphons fairly short; antero-lateral angle marked by a prominent spine; integument with minute reticulations; eyelobe minute; the whole body surface has a more or less scaly

appearance from the presence of small serrations or projections; there are no or only a few very short setae. The anterior pereon somites have the usual bifid dorsal lappets.

Antenna 1 (Fig. 41d) with basal segment sharply curved, shorter than second and third together. Maxilliped 2 (Fig. 41e, f) broadened, propodus with a continuous hyaline membrane on its inner edge, dactyl with basal spine not bifid and most distal spine distinctly longer than others. Maxilliped 3 (Fig. 41g) with basis distinctly longer than remaining segments together, carpus serrated along upper edge. Pereopod 1 (Fig. 41h) with basis about $\frac{3}{4}$ as long as remaining segments together, the next four segments about equal in length and $1\frac{1}{2}$ as long as the dactyl. Pereopod 2 (Fig. 41i) with basis about $\frac{2}{3}$ as long as remaining segments together, the ischium and carpus each with a terminal spine, the carpus not greatly longer than the merus. Uropod (Fig. 41j) with peduncle a little shorter than last two pleonites combined and little more than $1\frac{1}{4}$ as long as the endopod which is about $1\frac{1}{4}$ as long as the exopod.

The adult male shows the normal differences from the female and has no prominent spines on the carapace although the dorsum is somewhat serrated.

TYPE LOCALITY. 00° 46′ S–00° 46.5′ S, 29° 28′ W–29° 24′ W, 3459 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 356 : 1, allotype 1982 : 357 : 1, paratypes 1982 : 358 : 10.

REMARKS. This and the following species differ from most others in the genus by the armature of the dactyl of the second maxilliped, which has only three teeth apart from the terminal spine, resembling in this respect *P. tridentata*. Most other species have either four separate teeth or the proximal tooth is deeply cleft. *P. tridentata* has an elongate eyelobe.

DISTRIBUTION. Recorded at several stations off South-west Africa but also from single localities in the mid-Atlantic tropics and on the Gay Head–Bermuda transect, 1643–4693 m.

Procampylaspis hirta sp. nov.
(Fig. 42)

MATERIAL. BIOGAS III-DS41: 8 ad. ♂♂, 5 imm. ♂♂, 19 ad. ♀♀.

DESCRIPTION. Adult female, length 3·7 mm: carapace (Fig. 42a-c) less than twice as long as deep and about $1\frac{1}{3}$ as broad, smooth but with many fairly long setae and a single mid-dorsal small pointed spine; integument with a hexagonal pattern which is not pronounced and tending to catenary; pseudorostrum less than $\frac{1}{6}$ of total carapace length, not truncate in front; siphons fairly short; eyelobe small, pointed; antero-lateral angle defined by a sharp spine followed by some serrations. Anterior pereon somites with usual bifid dorsal lobes and with some longish setae. Pleon without spines but with a few short setae and small lateral serrations.

Antenna 1 (Fig. 42d) with basal segment curved, fairly stout; second and third segments successively shorter and more slender. Maxilliped 2 (Fig. 42e, f) with basal spine of dactyl not bifid, most distal spine longer than others but projecting inwards only little beyond the second from the base. Maxilliped 3 (Fig. 42g) with basis a little longer then remaining segments combined, the upper distal end slightly produced; the merus little broadened, longer than the carpus, slightly serrated on its lower edge, as is the upper edge of the carpus. Pereopod 1 (Fig. 42h) with basis distinctly shorter than remaining segments together, with a sharp spine at its lower distal end; the ischium about as long as the propodus and longer than the carpus, which is longer than the merus. Pereopod 2 (Fig. 42i) with basis about $\frac{2}{3}$ as long as remaining segments together, the carpus with a strong distal spine, about as long as ischium and merus together but only about $\frac{2}{3}$ as long as the dactyl. Uropod peduncle (Fig. 42j) about as long as last two pleonites together and more than $1\frac{1}{2}$ as long as the endopod, serrated on its outer edge and with a somewhat scaly appearance; the endopod has about 7 spines on the inner edge and a longer terminal spine; it is not much longer than the exopod.

Adult male differs from the female in the usual respects.

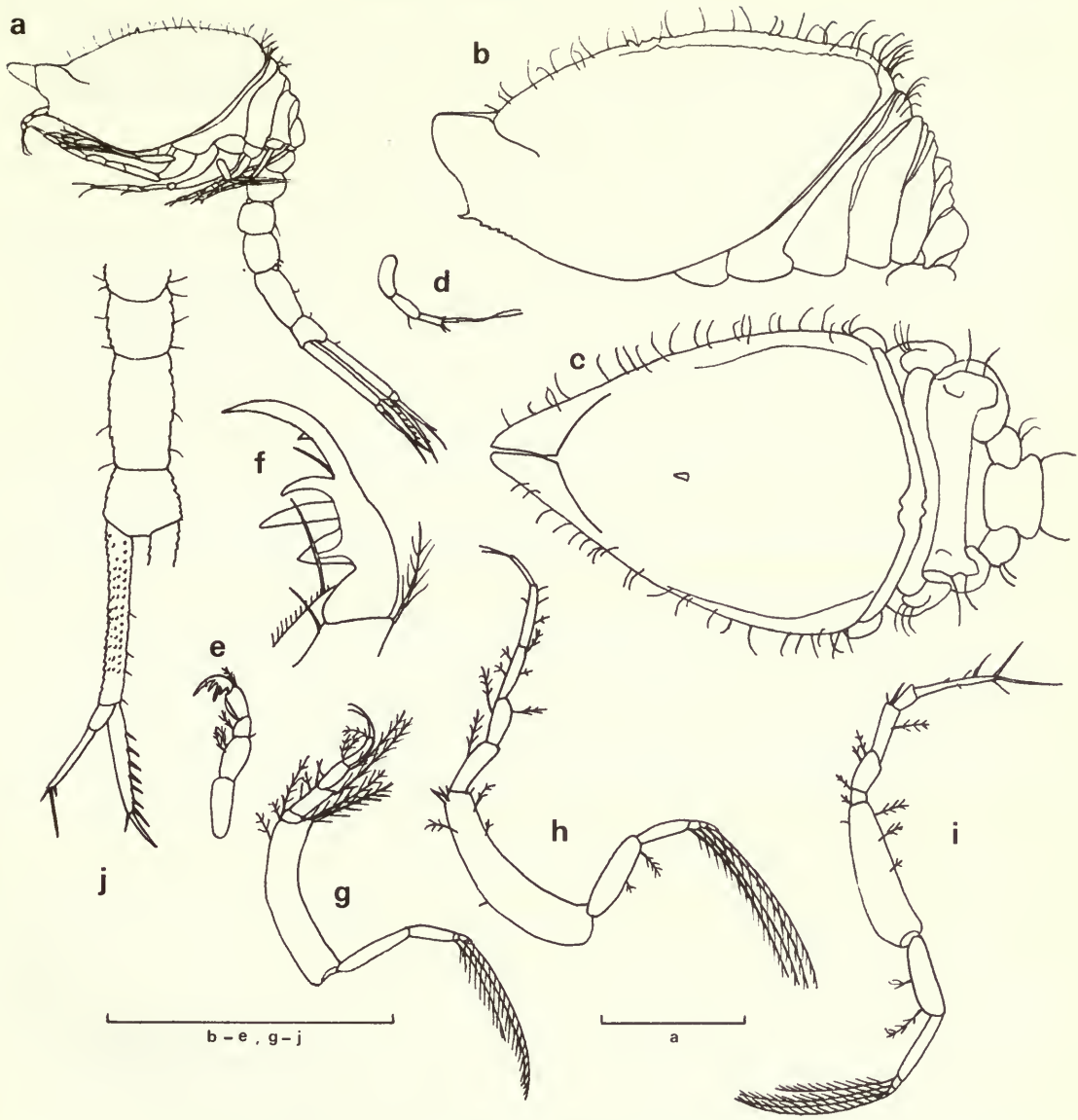

Fig. 42 *Procampylaspis hirta* ♀, (a) lateral view; (b) carapace and pereon from side; (c) carapace and pereon from above; (d) antenna 1; (e) maxilliped 2; (f) distal part of maxilliped 2 (further enlarged); (g) maxilliped 3; (h) pereopod 1; (i) pereopod 2; (j) uropod and end of pleon.

TYPE LOCALITY. 47° 28.3′ N, 9° 07.2′ W, 3548 m. Type specimens deposited in the Museum National d'Histoire Naturelle, Paris. Holotype ♀ no. Cu 216, allotype ♂ Cu 217, paratypes Cu 218.

REMARKS. *P. hirta* generally resembles *P. profunda* and has similarly a small rudimentary eyelobe but differs in having a small mid-dorsal spine and many fairly long setae on the carapace.

DISTRIBUTION. Numerous specimens were found at only a single station in the Bay of Biscay at a depth of 3548 m.

Key to the species of *Procampylaspis*

1 Carapace with many peculiar hooked setae ***bacescoi*** Reyss & Soyer, 1966
– Carapace with setae when present normally hair-like 2
2 Eyelobe rudimentary, small and scarcely elongated (Figs 40–42) 3
– Eyelobe normally developed or distinctly elongated (Figs 35–39). 9
3 Maxilliped 2 with proximal tooth on dactyl undivided (Figs 41, 42). 4
– Maxilliped 2 with proximal dactylar tooth bifid (Fig. 40) 5
4 Carapace without setae (Fig. 41) ***profunda*** sp. nov. (p. 265)
– Carapace with many fairly long setae (Fig. 42) ***hirta*** sp. nov. (p. 266)
5 Distal dactylar tooth of maxilliped 2 long, about three times as long as the medial tooth ***macronyx*** Hansen, 1920
– Distal dactylar tooth of maxilliped 2 less than twice as long as medial tooth (Fig. 40e) 6
6 Basis of maxilliped 2 with many spiniform scales ***maurini*** Bacescu & Muradian, 1972
– Basis of maxilliped 2 without scales or projections (Fig. 40d) 7
7 Carapace, pereon and pleon beset with many long setae ***arguini*** Bacescu & Muradian, 1972
– Setae when present on the integument are few and short (Fig. 40a) 8
8 Uropod peduncles scarcely longer than last two pleon somites together ***bonnieri*** Calman, 1906
– Uropod peduncles distinctly longer than the last three pleon somites together (Fig. 40a) ***ommidion*** sp. nov. (p. 263)
9 Eyelobe with lenses distinguishable 10
– No lenses visible in eyelobe 11
10 Carapace with two tubercles, one on either side dorso-laterally ***meridiana*** Jones, 1971
– Carapace with a single mid-dorsal tubercle ***thalassae*** Bacescu & Muradian, 1972
11 Eyelobe not much elongated, at most little more than $\frac{1}{3}$ as long as pseudorostrum and devoid of spines (Fig. 35d) 12
– Eyelobe more elongated, distinctly more than $\frac{1}{3}$ as long as pseudorostrum and often with one or more spines (Figs 36b, 37b, 38b, 39b) 13
12 Carapace without spines or tubercles; eyelobe broad at base (Fig. 35a, b, d) ***inermis*** sp. nov. (p. 255)
– Carapace with a strong mid-dorsal tubercle; eyelobe narrow ***unicornis*** Gamô, 1977
13 Eyelobe with a double row of small teeth or serrations (Fig. 39c) ***serratoculus*** sp. nov. (p. 260)
– Eyelobe unarmed or ending in a single or double spine or with a single row of teeth (Figs 36b, d, 37b, c, 38b-d) 14
14 Eyelobe with two spines side by side at or near its end 15
– Eyelobe unarmed, ending in a single spine, or with a single row of serrations . . 17
15 Carapace with two dorso-lateral tubercles on either side, each bearing two blunt spines; no other spines are present ***compressa*** Zimmer, 1907
– Carapace with a single mid-dorsal spine or none but no dorso-lateral tubercles; some small spines may be present dorso-laterally and laterally at the hind end 16
16 Eyelobe extending almost to the end of the pseudorostrum; second maxilliped with four teeth on the inner margin of the dactyl **armata** Bonnier, 1896
– Eyelobe extending to little more than half way along pseudorostrum; second maxilliped with only three teeth on inner margin of dactyl ***tridentata*** Stebbing, 1912
17 Eyelobe distinctly less than half as long as pseudorostrum and ending in a short spine (Fig. 37c) ***lutensis*** sp. nov. (p. 258)
– Eyelobe at least almost half as long as pseudorostrum (Figs 36b, c, 38b-d) 18
18 Carapace with two dorso-lateral tubercles, one on either side, each bearing a spine ***bituberculata*** Hansen, 1920
– Carapace with one mid-dorsal spine or none or many scattered spines (Figs 36a, c, 38b, d) 19
19 Dactyl of second maxilliped has the two proximal teeth long and narrow and deeply separated, the more distal tooth much more than half as long as the proximal; merus of third maxilliped with an outstanding spine of its inner margin ***sordida*** Hale, 1945
– Dactyl of second maxilliped has the proximal tooth bifid, not deeply cleft, with more distal part less or little more than half as long as the proximal; merus of third maxilliped without spine (Figs 36g, h, 38g, h) 20

20 Carapace with a prominent mid-dorsal spine; dactyl of second maxilliped with distal tooth little longer than the medial (Fig. 36a, c, g) ***procurrens*** sp. nov. (p. 256)
– Carapace without spines (♀) or with many dorsally and on its hind part; dactyl of second maxilliped with distal tooth distinctly longer than medial (Fig. 38b, d, g) ***acanthomma*** sp. nov. (p. 260)

Genus *CAMPYLASPIDES* Fage, 1929

Resembling *Campylaspis*. Mandible with the molar process prominent, styliform. Second maxilla with one lobe on the basis provided with one or more setae. Second maxilliped with the dactyl in the form of a trident, articulated at the distal end of the propodus.

The peculiar shape of the second maxilliped, especially the three-pronged dactyl, is the chief feature distinguishing this genus from *Campylaspis*. There are now three species known, all from the deep Atlantic.

Campylaspides grandis Fage, 1929

MATERIAL. MBAUK-44: 1 imm. ♀. BIOGAS VI-DS86: 1 imm. ♀. CP23: 2 ad. ♀♀.

DISTRIBUTION. The original record was of a single female from off the Azores in 1482 m. It is now recorded from the Bay of Biscay between 1739 and 1980 m. The male remains unknown.

Campylaspides spinifera Jones, 1973

MATERIAL. AII31-167: 3 imm. ♂♂, 1 ad. ♀, 1 imm. ♀, 7 juv. Kn25-291: 1 juv. 293: 2 ad. ♂♂, 2 ad. ♀♀, 4 juv.

DISTRIBUTION. Two adult males were recorded from a station off the coast of tropical Brazil in 587 m. Further records are of both sexes from another station off Brazil in 943–1007 m and from two stations off Surinam in 1500 m and 3859–3868 m respectively.

Campylaspides canariensis sp. nov.
(Fig. 43)

MATERIAL. IOS-6696: 1 imm. ♂, 4 ad. ♀♀, 1 imm. ♀. 6697: 1 ad. ♂, 1 imm. ♀, 1 juv. 6701: 2 imm. ♂♂, 1 ad. ♀, 1 imm. ♀, 1 juv. 6704: 1imm. ♀. 6711: 1 juv. BIOGAS IV-DS52: 1 imm. ♀.

DESCRIPTION. Adult female, length 4·9 mm: carapace (Fig. 43a) smooth with scattered long setae towards front, nearly $2\frac{1}{2}$ as long as deep, covering anterior pereon somites; pseudorostrum long and prominent, nearly $\frac{1}{4}$ of total carapace length; antennal notch well excavated with prominent antero-lateral angle below, defined by a spine; eyelobe rudimentary. Pereon and anterior pleon somites have hyaline dorso-lateral spines and a few short setae.

Antenna 1 (Fig. 43b) with basal segment slender, a little curved, not quite as long as second and third segments together; the second segment about $1\frac{1}{2}$ as long as the third. Maxilliped 2 (Fig. 43c) with ischium distinct, dactyl prolonged into three long spines about equal in length; the propodus with one long distal spine and a single spine on the carpus. Maxilliped 3 (Fig. 43d) with basis fairly stout, strongly curved, distinctly shorter than remaining segments together; the merus is longer than the carpus and neither is slender; the propodus is shorter than the carpus and more than twice as long as the dactyl. Pereopod 1 (Fig. 43e) with basis about $\frac{3}{4}$ as long as remaining segments together; the merus is expanded downwards distally and is shorter than the narrow carpus, which is about as long as the propodus and about $1\frac{1}{2}$ as long as the still more slender dactyl. Pereopod 2 (Fig. 43f) with basis less than $\frac{2}{3}$ as long as remaining segments together; the merus is about $\frac{1}{3}$ as long as the carpus, which is a little shorter than the slender tapering dactyl. Uropod (Fig. 43g) with peduncle unarmed except for a few short setae, distinctly longer than the last two pleonites together and nearly twice as long as the endopod. The endopod has two inner spines and a longer terminal spine and is about equal in length to the exopod.

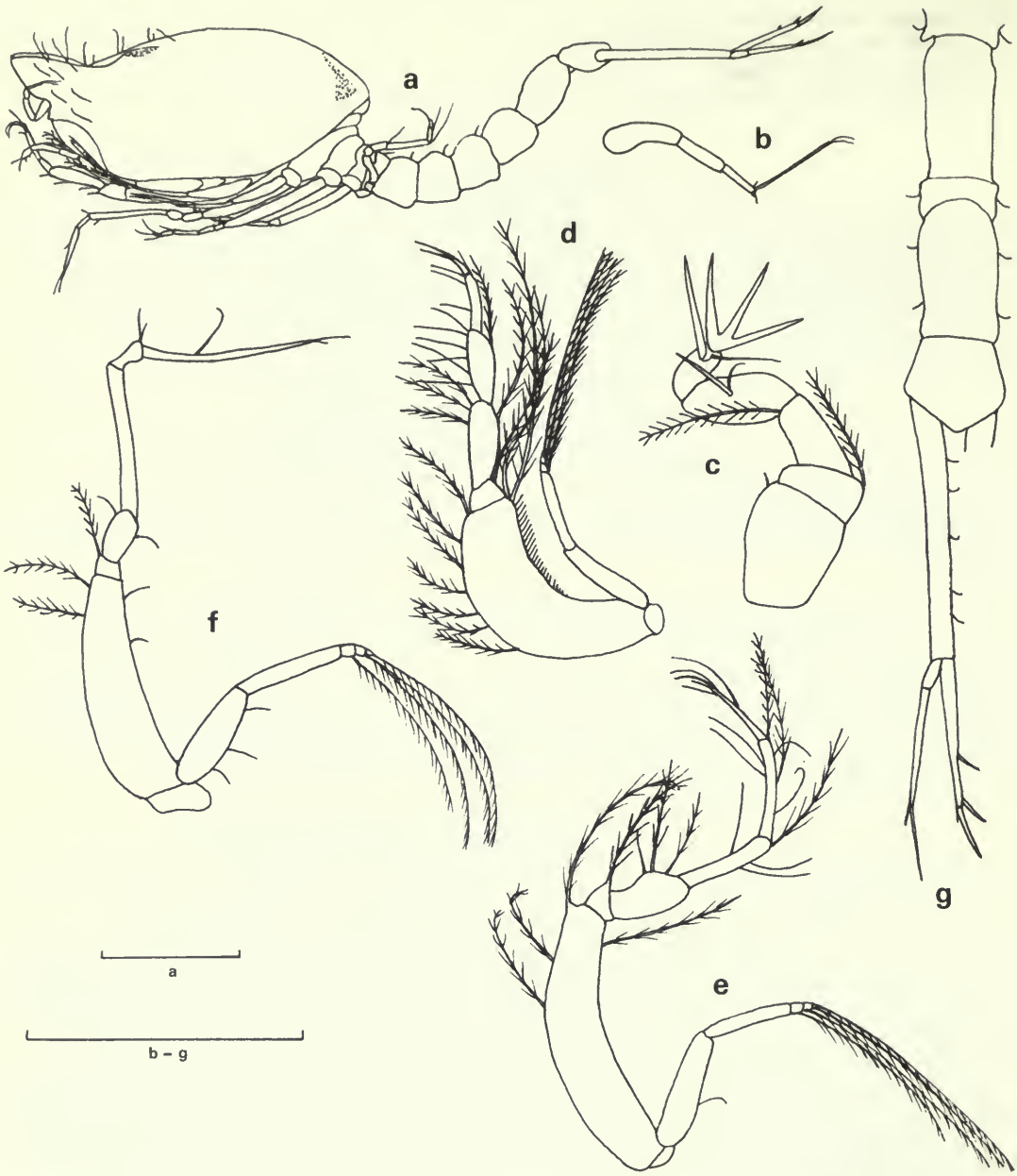

Fig. 43 *Campylaspides canariensis* ♀, (a) lateral view; (b) antenna 1; (c) maxilliped 2; (d) maxilliped 3; (e) pereopod 1; (f) pereopod 2; (g) uropod and end of pleon.

Adult male generally similar to female. The flagellum of the second antenna reaches at least beyond the hind end of the pereon. It is probably broken short in the only adult available.

TYPE LOCALITY. 28° 06′ N, 13° 28′ W, 1780 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982:359:1, allotype 1982:360:1, paratypes 1982 : 361 : 2.

REMARKS. From *C. spinifera* this species is easily separated by the lack of carapace spinulation. Amongst other differences, the carpus of the third maxilliped is broad instead of narrow. *C. grandis* has several strong spines on the carpus of the second maxillipeds, not present in *C. canariensis*; there are many spines on the merus and carpus of the third maxillipeds in *C. grandis* which are lacking in *C. canariensis*; in the latter, the outer ramus of the uropod is almost as long as the inner instead of being much shorter and the inner ramus is more than half as long as the peduncle whereas in *C. grandis* it is much less than half as long.

DISTRIBUTION. Found at several stations off the Canary Islands and at one in the Bay of Biscay, between 1564 and 2988 m depth.

Genus *CAMPYLASPIS* G. O. Sars, 1865

Carapace strongly vaulted in the female, often bulging over the anterior pereon somites. Antero-lateral angles of the carapace not strongly produced. Eye unpaired and often rudimentary, seldom elongated. Mandible with the molar process styliform. The second maxilla reduced to a simple plate without movable endites. The first maxilliped reduced, with only three segments, the terminal very small. The second maxilliped with the propodus articulated at nearly a right-angle to the carpus and ending in a broad seta, the dactyl short and ending in two or more diverging spines. The first pereopod with the ischium not specially elongated.

Including the 5 new species described in this paper, there are now approximately 107 species in the genus.

Muradian (1979*b*) has divided the genus into two subgenera on the basis of the form of the second maxilla, which may have its distal edge broad and truncate or pointed. Each subgenus is again divided into several groups according to the shape and armature of the maxillipeds. A detailed study with comparative figures would be necessary before these proposals meet with general acceptance since the second maxillae and first maxillipeds have not been described in many species, but when this has been done it would no doubt provide excellent material for cluster analysis.

Campylaspis alba Hansen, 1920

MATERIAL. IOS-7709 # 72: 1 ad. ♂, 1 ad. ♀, 3 imm. ♀♀. 7709 # 73: 3 ad. ♂♂, 5 ad. ♀♀, 1 juv. 7709 # 85: 1 imm. ♀. SMBA-ES15: 1 imm. ♂, 5 imm. ♀♀, 1 juv. ES18: 1 imm. ♂, 1 imm. ♀, 1 juv. ES20: 2 ad. ♂♂, 6 imm. ♂♂, 1 ad. ♀, 1 imm ♀. ES22: 2 imm. ♂♂, 1 imm. ♀, 1 juv. ES20: 2 ad. ♂♂, 6 imm. ♂♂, 1 ad. ♀, 1 imm. ♀. ES22: 2 imm. ♂♂, 1 imm. ♀, 2 juv. *Thalassa* 73-Z426: 1 imm ♂. Z429: 2 ad. ♀♀, 2 imm. ♀♀. BIOGAS III-DS41: 5 ad. ♀♀. All59-211: 1 ad. ♂, 7 ad. ♀♀. Ch106-313: 1 ad. ♀, 3 juv.

DISTRIBUTION. Further records (additional to those in Jones, 1974) include a station in the Mediterranean and range between 506 and 3548 m depth.

Campylaspis nitens Bonnier, 1896

MATERIAL. SMBA-ES4: 5 ad. ♂♂, 3 imm. ♂♂, 20 ad. ♂♂, 14 imm. ♀♀. ES6: 3 imm. ♂♂, 1 ad. ♀, 7 imm. ♀♀, 1 juv. ES10: 6 ad. ♂♂, 35 ad. ♀♀, 2 juv. ES12: 1 ad. ♂, 4 imm. ♂♂, 2 ad. ♀♀, 3 imm. ♀♀. ES18: 2 imm. ♂♂, 1 imm. ♀. ES20: 1 imm. ♂, 1 ad. ♀. BIOGAS I-DS09: 1 ad. ♂, 1 ad. ♀. POLYGAS-DS16: 1 ad. ♂, 2 ad. ♀♀. DS18: 1 imm. ♂. DS25: 3 ad. ♀♀. DS26: 1 ad. ♂, 1 imm. ♂, 6 ad. ♀♀. BIOGAS III-DS35: 1 imm. ♂. BIOGAS IV-DS51: 10 ad. ♂♂, 8 ad. ♀♀, 3 imm. ♀♀. DS52: 2 ad. ♀♀, 1 imm. ♀. BIOGAS VI-DS86: 2 ad. ♂♂, 1 imm. ♂, 3 ad. ♀♀. DS87: 1 ad. ♂, 1 imm. ♂, 2 ad. ♀♀. CP23: 1 imm. ♂, 1 imm. ♀. CP24: 1 ad. ♀. CP25: 1 imm. ♂, 1 juv.

DISTRIBUTION. Now recorded from many stations west of Scotland and in the Bay of Biscay between 1284 and 2900 m.

Campylaspis nuda Jones, 1974

MATERIAL. All60-240: 2 ad. ♂♂, 4 ad. ♀♀, 2 imm. ♀♀, 1 juv. 264. 1 ad. ♀. Kn25-293: 1 ad. ♂, 2 imm. ♂♂, 10 ad. ♀♀, 2 imm. ♀♀. 297: 1 imm. ♀.

DISTRIBUTION. Originally recorded from off tropical Brazil, it has now been found off the Argentine and off Surinam between 500 and 2323 m depth. In some specimens, the carapace has a slight antero-dorsal prominence on either side.

Campylaspis paeneglabra Stebbing, 1912

MATERIAL. BIOGAS II-DS33: 4 ad. ♂♂, 4 imm. ♂♂, 8 imm. ♀♀, 2 juv. DS34: 1 ad. ♂.

DISTRIBUTION. Found at two stations in the Bay of Biscay between 1031 and 2338 m. The only other record was that of Stebbing off South Africa in 805 m.

Campylaspis mauritanica Bacescu and Muradian, 1972

MATERIAL. *Thalassa* 73-Z398: 1 ad. ♀.

DISTRIBUTION. The original record was from the Mauritanian coast in 270 m and it is now recorded from a single station in the Bay of Biscay in 330 m.

Campylaspis rubicunda (Lilljeborg, 1855)

MATERIAL. IOS-7709 # 72: 2 ad. ♀♀. SMBA-ES2: 1 imm. ♀. ES4: 1 juv. ES12: 1 imm. ♀. *Thalassa* 73-Z400: 1 ad. ♀. POLYGAS-DS15: 1 ad. ♀. DS16: 1 imm. ♂, 2 ad. ♀♀, 2 imm. ♀♀, 1 juv. BIOGAS IV-DS52: 1 imm. ♀. BIOGAS V-DS65: 3 imm. ♀♀. BIOGAS VI-CP23: 1 ad. ♀, 3 juv.

DISTRIBUTION. Further records of this species include several Biscay stations and extend down to 2857 m.

Campylaspis laevigata Jones, 1974

MATERIAL. *Thalassa* 70-W357: 3 imm. ♂♂, 3 imm. ♀♀, 1 juv. BIOGAS I-DS14: 2 imm. ♂♂, 2 imm. ♀♀. AII60-236: 2 imm. ♂♂.

DISTRIBUTION. Originally recorded from off SW. Africa and from the Bay of Biscay, the additional stations are from off the Argentine coast and Biscay between 500 and 1560 m.

Campylaspis bonetti Bacescu and Muradian, 1972

MATERIAL. *Thalassa* 70-W357: 1 imm. ♂, 3 imm. ♀♀.

DISTRIBUTION. First recorded from the coast of Mauritania between 52 and 96 m depth, it has now been found in Biscay at 1000 m.

Campylaspis glabra Sars, 1879

MATERIAL. *Thalassa* 73-Z399: 1 ad. ♀, 1 imm. ♀. Z414: 1 ad. ♀, 5 imm. ♀♀. Z415: 1 ad. ♀. Z420: 1 imm. ♀. Z422: 1 imm. ♀. Z424: 1 ad. ♀, 2 juv. Z434: 2 juv. Z437: 1 ad. ♀. Z458: 2 ad. ♀♀. BIOGAS I-DS01: 1 imm. ♂. DS09: 1 ad. ♀. NORBI-CP11: 2 imm. ♂♂, 1 ad. ♀. AII59-211: 7 ad. ♂♂, 6 imm. ♂♂, 68 ad. ♀♀, 10 imm. ♀♀, 4 juv.

DISTRIBUTION. Further records are within its previously known range both horizontal and vertical.

Campylaspis vitrea Calman, 1906

MATERIAL. *Thalassa* 70-W357: 1 imm. ♂, 1 imm. ♀, 3 juv. W371: 1 imm. ♂, 1 ad. ♀, 1 imm. ♀. *Thalassa* 72-Y374: 1 imm. ♀. *Thalassa* 73-Z426: 1 imm. ♀. AII59-211: 1 ad. ♂, 2 imm. ♂♂. Kn25-293: 2 ad. ♂♂, 11 imm. ♂♂, 20 ad. ♀♀, 23 imm. ♀♀. 295: 1 imm. ♂, 1 imm. ♀, 1 juv. 297: 1 imm. ♂, 2 imm. ♀♀. 299: 2 imm. ♂♂, 4 ad. ♀♀, 1 imm. ♀, 1 juv.

DISTRIBUTION. Former records were from the Mediterranean and Biscay and also from between North Carolina and Florida (Muradian, 1976). Now recorded also from off Surinam and from depths between 500 and 2000 m.

Campylaspis macrophthalma Sars, 1879

MATERIAL. *Thalassa* 73-Z424: 1 ad. ♀, 1 juv. Z427: 1 imm. ♀. Z456: 1 imm. ♀. BIOGAS I-DS01: 1 ad. ♂. AII59-211: 37 ad. ♂♂, 120 ad. ♀♀, 22 imm. ♀♀.

DISTRIBUTION. As well as from the Mediterranean and Biscay, this species was also recorded from off Morocco by Bacescu and Muradian (1972*b*). I have examined specimens from the English Channel and the North Sea. The present records were from depths between 280 and 509 m, extending its known range downwards.

Campylaspis johnstoni Hale, 1937

MATERIAL. AII60-237: 1 mm. ♀, 1 juv. 239: 2 imm. ♂♂, 41 imm. ♀♀. 240: 1 ad. ♂, 9 imm. ♂♂, 22 ad. ♀♀, 29 imm. ♀♀, 34 juv. 242: 1 imm. ♀. 245: 29 imm. ♀♀, 27 juv. 262: 2 imm. ♀♀, 1 juv.

DISTRIBUTION. Earlier records were from the Antarctic in 193 m and Kerguelen (Ledoyer, 1977) and also from off the Argentine coast, 424–428 m (Muradian, 1976). The present records were from deeper water off Argentina between 1011 and 4402 m.

Campylaspis ovalis Stebbing, 1912

MATERIAL. Kn25-297: 1 imm. ♀.

DISTRIBUTION. Found originally off South Africa in 805 m, a single specimen from 500 m off the coast of Surinam is now attributed to this species.

Campylaspis sticta Jones, 1974

MATERIAL. AII60-240: 1 ad. ♂, 8 ad. ♀♀, 2 imm. ♀♀, 3 juv.

DISTRIBUTION. Formerly recorded from a station off SW. Africa, 1007–1014 m, a further 14 specimens were obtained off the Argentine coast, 2195–2323 m.

Campylaspis costata Sars, 1865

MATERIAL. IOS-7709 # 66: 1 ad. ♂. 7709 # 72: 1 ad. ♀. 7709 # 73: 1 ad. ♂, 2 ad. ♀♀. SMBA-ES4: 1 imm. ♀. ES6: 1 ad. ♀. ES129: 1 imm. ♂. POLYGAS-DS15: 1 imm. ♀. BIOGAS II-DS31: 2 ad. ♂♂, 4 imm. ♂♂, 4 ad. ♀♀, 5 imm. ♀♀, 8 juv. BIOGAS IV-DS51: 1 imm. ♂. BIOGAS VI-DS74: 1 imm. ♂. Kn25-303: 1 imm. ♂.

DISTRIBUTION. Previous records were from Norway to the British Isles, 23–478 m, and off NE. America down to 1470 m; it is now recorded from a station off Surinam and several west of Scotland and in Biscay at depths between 2000 and 2900 m.

Campylaspis scuta sp. nov.
(Fig. 44)

MATERIAL. Kn25-297: 2 ad. ♀♀.

DESCRIPTION. Adult female, length 3·7 mm: carapace (Fig. 44a, b) raised dorsally, about 1½ as long as deep and slightly less as broad, with a rounded prominence bearing a small spine on either side behind the frontal lobe and about four teeth on either side below these and extending farther back; there are also a few dorsal spines placed in pairs behind the frontal lobe; the integument is loosely reticulated and a number of prominent dark red chromatophores are visible; there are a few short setae dorsally; the pseudorostrum is less than 1/7 of the total carapace length, with the siphon projecting for about the same distance; the antennal notch is slightly excavated and the antero-lateral angle defined by a tooth with a diminishing series behind it; the eyelobe is moderately long, rounded in front and with sides nearly parallel. The pereon is smooth and without dorsal elevations. The pleon somites are serrated dorsally and laterally.

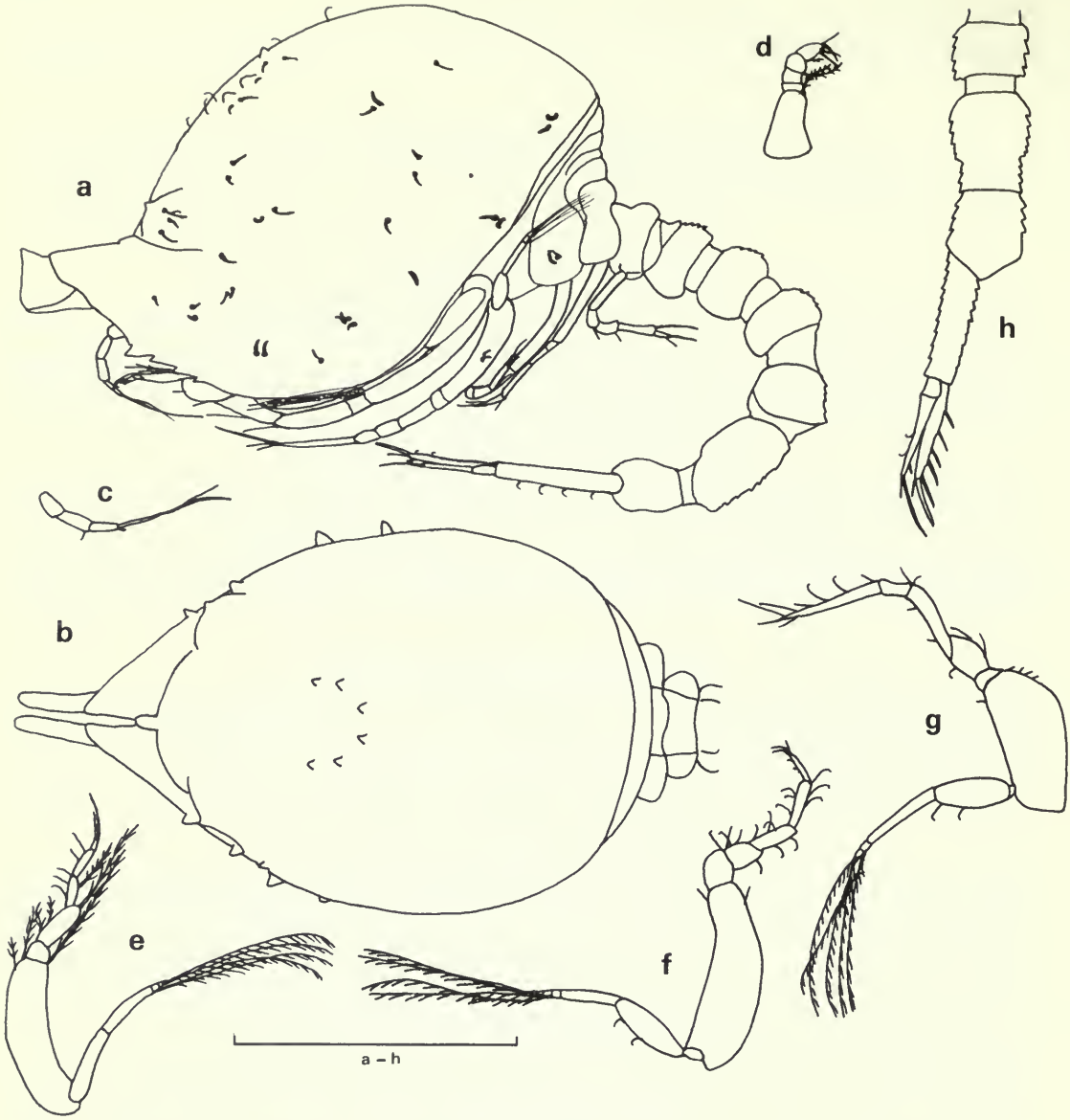

Fig. 44 *Campylaspis scuta* ♀, (a) lateral view; (b) carapace from side; (c) antenna 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereopod 1; (g) pereopod 2; (h) uropod and end of pleon.

Antenna 1 (Fig. 44c) with basal segment of peduncle short and broad, shorter than the second and about as long as the third. Maxilliped 2 (Fig. 44d) with basal seta not specially thickened; dactyl with only two slender spines. Maxilliped 3 (Fig. 44e) with basis longer than remaining segments together, the merus unarmed and much longer than the carpus or propodus. Pereopod 1 (Fig. 44f) with basis about as long as remaining segments together, ischium and merus about equal in length and shorter than the subequal carpus and propodus. Pereopod 2 (Fig. 44g) with basis barely 2/3 as long as remaining segments together, the ischium short, the merus broad and little more than half as long as the carpus which is about three times as long as the propodus and somewhat shorter than the gradually tapering dactyl. Uropod (Fig. 44h) with peduncle short, about $1\frac{1}{2}$ as long as last pleonite, serrated on both

edges, distinctly longer than the rami; the endopod with 5 slender spines on its inner edge and a longer terminal spine, about as long as the exopod.

Adult male unknown.

TYPE LOCALITY. 7° 45.3′ N, 52° 24′ W, 508–523 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 362 : 1, paratype 1982 : 363 : 1.

REMARKS. In the key in Jones (1974), *C. scuta* would run out near *C. affinis* Sars, but there are many obvious differences, notably in the second maxillipeds and uropods.

DISTRIBUTION. Two adult females were found at 500 m depth off the coast of Surinam.

Campylaspis spinosa Calman, 1906

MATERIAL. Kn25-293: 11 imm. ♂♂, 18 ad. ♀♀, 28 imm. ♀♀.

DISTRIBUTION. Earlier records were from the Mediterranean, off the Canaries, SW. Africa and tropical Brazil, 587–2924 m depth. It is now recorded also from off Surinam in 1500 m.

Campylaspis laticarpa Hansen, 1920

MATERIAL. *Thalassa* 73-Z430: 1 imm. ♀. Z459: 1 imm. ♂. BIOGAS VI-CP23: 1 imm. ♂.

DISTRIBUTION. Previously recorded by Hansen south-west of the Faroes between 810 and 942 m depth, it is now recorded from Biscay between 1080 and 1980 m.

Campylaspis pilosa Jones, 1974

MATERIAL. All60-239: 3 ad. ♀♀, 1 imm. ♀. Kn25-293: 2 ad. ♂♂, 4 ad. ♀♀, 1 imm. ♀. 297: 3 ad. ♂♂, 5 imm. ♂♂, 13 ad. ♀♀, 3 juv. 299: 4 imm. ♂♂, 5 ad. ♀♀, 7 imm. ♀♀, 1 juv.

DISTRIBUTION. First recorded from off tropical Brazil in 587 to 1007 m depth and now from off the Argentine and Surinam between 500 and 2000 m.

Campylaspis affinis Sars, 1870

MATERIAL. SMBA-ES27: 1 ad. ♂, 2 imm. ♂♂. ES56: 1 imm. ♂. ES59: 1 imm. ♂. ES118: 1 ad. ♂. ES129: 1 ad. ♂, 1 ad. ♀, 1 imm. ♀, 2 juv. ES135: 2 imm. ♂♂, 1 ad. ♀, 1 imm. ♀. ES137: 1 ad. ♂, 2 imm. ♂♂, 2 juv. ES140: 3 ad. ♀♀. ES147: 3 imm. ♂♂, 5 imm. ♀♀, 1 juv. BIOGAS IV-DS62: 1 imm. ♂. Ch106-321: 1 ad. ♀.

DISTRIBUTION. Described by Sars from off Norway, it is now recorded from west of Scotland and Biscay between 2175 and 2920 m.

Campylaspis quadriplicata Lomakina, 1968

MATERIAL. All60-240: 2 imm. ♀♀. 245: 4 imm. ♀♀.

DISTRIBUTION. Described from the Antarctic between 165 and 180 m depth and recorded by Muradian (1976) from off the Argentine and Chile in 470 to 1475 m, it is now recorded also from the Argentine in 2323 to 2707 m.

Campylaspis valida sp. nov.
(Fig. 45)

MATERIAL. Kn25-297: 2 ad. ♀♀.

DESCRIPTION. Adult female, length 7·2 mm: carapace (Fig. 45a-c) about $1\frac{2}{3}$ as long as high and nearly $1\frac{1}{2}$ as wide, overlapping the anterior pereon behind, with several pairs of dorso-lateral protuberances and hollows; on either side a ridge extends upwards and backwards from the antennal notch, being joined by another less well defined, running obliquely backwards from behind the frontal lobe, and dividing into two farther back, the upper branch running first upwards and then downwards to end towards the rear of the carapace and the

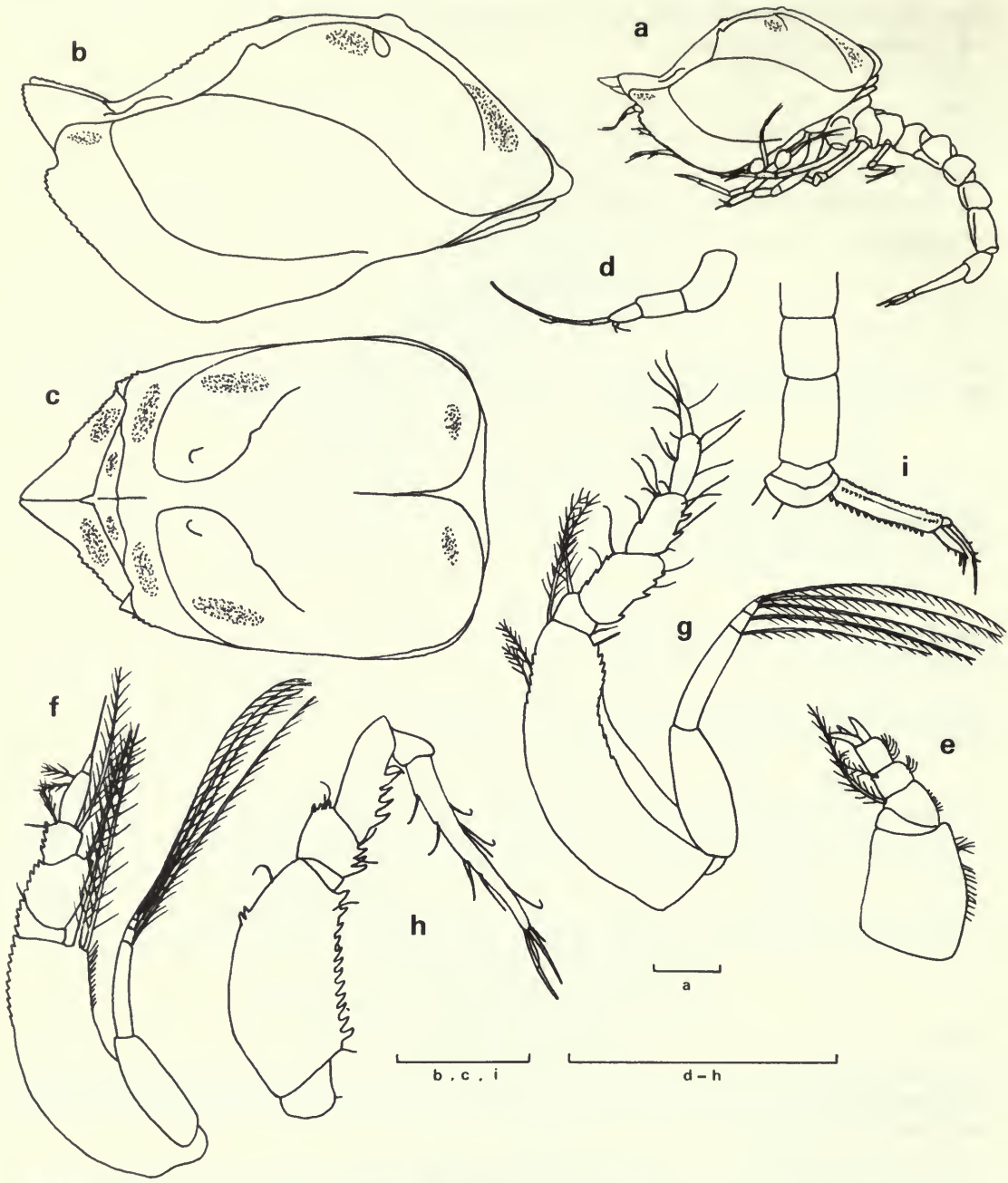

Fig. 45 *Campylaspis valida* ♀, (a) lateral view; (b) carapace from side; (c) carapace from above; (d) antenna 1; (e) maxilliped 2; (f) maxilliped 3; (g) pereopod 1; (h) pereopod 2; (i) uropod and end of pleon.

lower branch running downwards and then recurving upwards to meet its fellow mid-dorsally just in front of the hind end of the carapace; from the side the dorsum behind the frontal lobe appears serrated; the pseudorostrum is triangular, slightly raised dorsally, serrated below, siphons short; the antennal notch is well excavated and the antero-lateral angle prominent but rounded, with small serrations extending backwards; the eyelobe is rudimentary, narrow and pointed. The pereon and pleon somites are comparatively smooth.

Antenna 1 (Fig. 45d) with basal segment stout, slightly serrated below, the next two segments of the peduncle decreasing in length and thickness. Maxilliped 2 (Fig. 45e) with ischiobasis short and robust, without a thickened distal seta; the dactyl with two equal spines. Maxilliped 3 (Fig. 45f) with basis 1½ as long as remaining segments together, serrated distally below, the merus broad and produced above; ischium, merus and carpus are serrated below; dactyl very short. Pereopod 1 (Fig. 45g) with basis stout, distally serrated above and below, distinctly longer than remaining segments together; the merus longer than the carpus and both segments with a few fairly large spines or serrations on their upper edges; propodus a little shorter than the carpus but nearly twice as long as the dactyl. Pereopod 2 (Fig. 45h) with basis stout, little more than half as long as remaining segments together; the carpus is about twice as long as the merus and less than ⅔ as long as the slightly tapering dactyl; basis, merus and carpus each has a row of stout spines along its upper edge and there are two spines each on the lower edges of the basis and merus. Uropod (Fig. 45i) fairly short with peduncle strongly serrated on either side and dorsally towards its base, shorter than last two pleonites together; the endopod is little more than ⅓ as long as the peduncle and shorter than the exopod.

Adult male unknown.

TYPE LOCALITY. 7° 45.3′ N, 52° 24′ W, 508–523 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 364 : 1, paratype 1982 : 365 : 1.

REMARKS. *C. valida* has some general resemblance to *C. bulbosa* Jones and would key out near to it in Jones (1974). However, there are many differences in carapace sculpturing and in the armature of the appendages.

DISTRIBUTION. Two adult females were found off Surinam in 500 m.

Campylaspis selvakumarani (Bacescu and Muradian, 1974) comb. nov.

Floridocuma selvakumarani Bacescu & Muradian, 1974
Campylaspis paucispina Jones, 1974

MATERIAL. SMBA-ES4: 1 ad. ♂, 9 ad. ♀♀. ES12: 3 ad. ♂♂, 5 ad. ♀♀, 8 imm. ♀♀. ES15: 1 ad. ♀. ES18: 2 imm. ♀♀. ES20: 6 ad. ♀♀, 1 imm. ♀, 3 juv. BIOGAS I-DS13: 1 imm. ♀. POLYGAS-DS15: 1 ad. ♂, 4 ad. ♀♀, 2 imm. ♀♀. DS18: 1 ad. ♂, 1 ad. ♀, 4 imm. ♀♀. BIOGAS III-DS35: 1 imm. ♀. Ch106-313: 1 imm. ♂, 1 juv.

REMARKS. Bacescu and Muradian erected a new genus for this species on the grounds of the club-shaped distal seta on the basis of its second maxilliped, of which the propodus is said to have a different articulation against the carpus from *Campylaspis.* I am unable to find the rudimentary exopods on pereopods 3 and 4 described by Bacescu and Muradian and believe their specimen to have been an immature male. Since this shape of seta is now known to be shared with several other species of *Campylaspis,* which have no other special features in common, and the propodus does not seem to me to be unusual in shape, I am unable to accept *Floridocuma.*

The second antennal flagellum of the male is short and not long, as stated in error by Jones (1974).

DISTRIBUTION. Originally described from south of Cape Cod in 2085 m depth and also found in about the same locality between 1102 and 2496 m, it is now recorded within this depth range from west of Scotland and Biscay.

Campylaspis gamoi sp. nov.
(Fig. 46)

MATERIAL. POLYGAS-DS16: 3 imm. ♀♀.

DESCRIPTION. Adult female, length 3·5 mm: carapace (Fig. 46a-c) about 1⅔ as long as deep and 1½ as broad, smooth except for a blunt prominence on either side of the frontal lobe

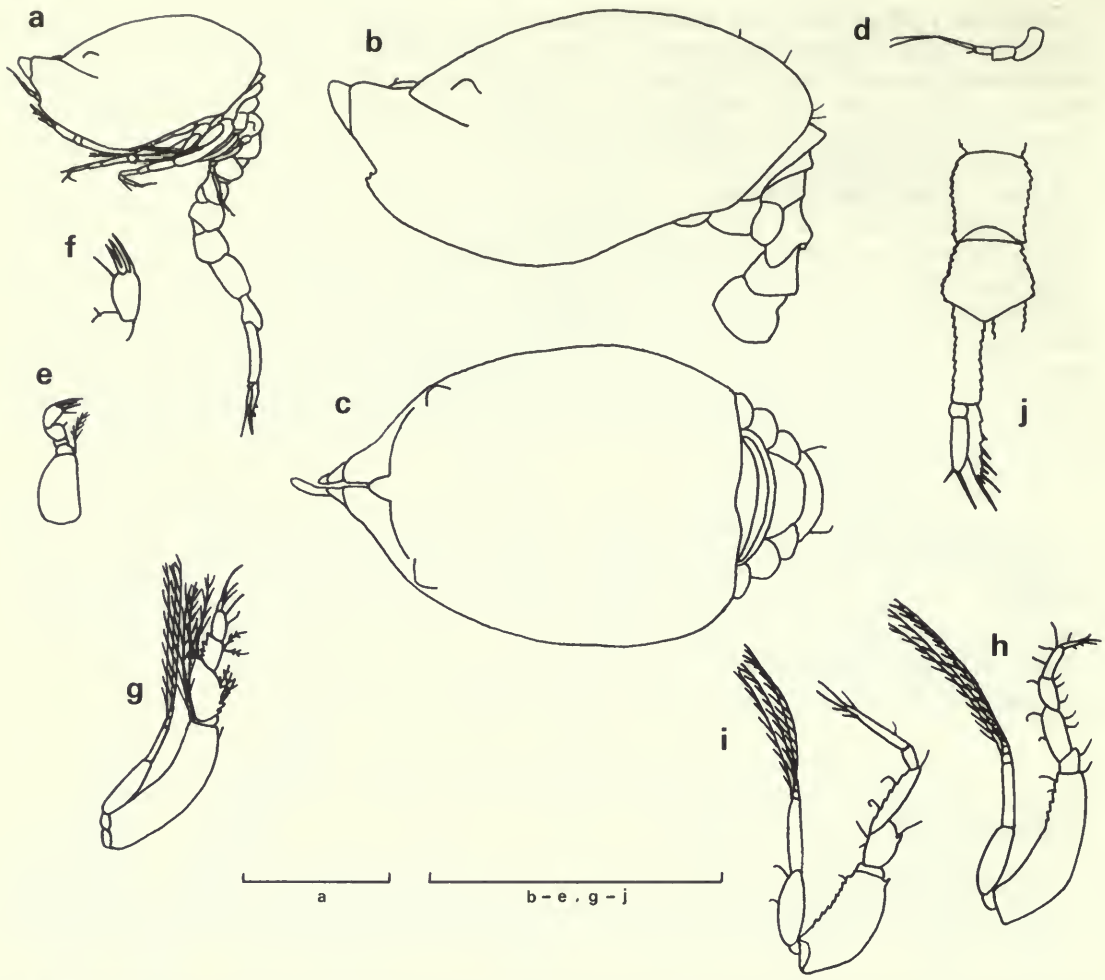

Fig. 46 *Campylaspis gamoi* ♀, (a) lateral view; (b) carapace and pereon from side; (c) carapace and pereon from above; (d) antenna 1; (e) maxilliped 2; (f) distal part of maxilliped 2 (further enlarged); (g) maxilliped 3; (h) pereopod 1; (i) pereopod 2; (j) uropod and end of pleon.

and a few short setae; the integument is hexagonally reticulated; the pseudorostrum is less than ⅓ of the total carapace length, truncated in front, with a well excavated antennal notch below; the antero-lateral angle is distinct with a few slight serrations; siphons short; the eyelobe is fairly large and broad, rounded in front. The posterior pleon somites are serrated laterally.

Antenna 1 (Fig. 46d) with basal segment curved, not broad, nearly as long as second and third together. Maxilliped 2 (Fig. 46e, f) with ischiobasis broad at base; dactyl with two equal spines. Maxilliped 3 (Fig. 46g) with basis not widened, much longer than remaining segments together, merus fairly broad and with several short spines below and one distally above; carpus about half as long as merus and about as long as propodus, with several spines or serrations on its upper edge. Pereopod 1 (Fig. 46h) with basis very little longer than remaining segments together, with some serrations on its distal upper edge; the merus is more than twice as long as the ischium and about 1½ as long as the subequal carpus or propodus. Pereopod 2 (Fig. 46i) with basis broad, little more than half as long as remaining segments together, serrated along its upper edge and with a spine on its lower edge distally; the merus

is broadened, with a spine on the lower edge; the carpus is almost twice as long as the merus, serrated along its upper edge, and about equal in length to the dactyl, which is little tapered. Uropods (Fig. 46j) short, peduncle little longer than last pleonite, serrated on either edge, barely $1\frac{1}{4}$ as long as the endopod, which is rather broad and scarcely longer than the exopod.

TYPE LOCALITY. 47° 36.1′ N, 8° 40.5′ W, 2325 m. Type specimens deposited in the Museum National d'Histoire Naturelle, Paris. Holotype ♀ no Cu 219, paratype Cu 220.

REMARKS. In carapace shape but in little else, *C. gamoi* resembles *C. pilosa,* having a single pair of blunt prominences at the sides of the frontal area. However, it is easily distinguished by the lack of setae on the carapace, the size of the eyelobe, the comparative shortness of the uropods and many details of the appendages.

DISTRIBUTION. Three immature females were found at a single station in Biscay, depth 2325 m.

Campylaspis undata Sars, 1865

MATERIAL. *Thalassa* 73-Z452: 1 juv. NORBI-CP11: 2 imm. ♂♂.

DISTRIBUTION. Recorded from the coast of Norway and south-west of the Faroes, 183–1185 m, it is now further recorded from Biscay in 1470 m.

Campylaspis sulcata Sars, 1870

MATERIAL. SMBA-ES23: 1 juv. *Thalassa* 73-Z400: 1 imm. ♀, 2 juv. Z413: 1 imm. ♂, 2 imm. ♀♀. Z414: 1 ad. ♂, 4 ad. ♀♀. Z416: 3 ad. ♂♂, 1 imm. ♂, 2 ad. ♀♀, 1 imm. ♀. Z417: 1 imm. ♂, 3 ad. ♀♀, 3 imm. ♀♀. Z420: 1 ad. ♂, 1 ad. ♀. Z421: 1 imm. ♂, 1 ad. ♀, 1 imm. ♀. Z424: 3 juv. Z425: 2 ad. ♂♂, 1 ad. ♀. Z426: 1 ad. ♀, 1 juv. Z427: 1 ad. ♂, 2 ad. ♀♀. Z431: 1 imm. ♀. Z435: 1 ad. ♀, 1 imm. ♀. Z441: 1 juv. Z456: 1 ad. ♀. Z458: 2 imm. ♂♂, 3 imm. ♀♀. NORBI-CP11: 2 imm. ♀♀. AII59-211: 3 imm. ♀♀.

DISTRIBUTION. Previous records were from Norway, west of Ireland and the Mediterranean in about 130 to 650 m depth; it is now recorded also from Biscay down to 1400 m.

Campylaspis valleculata Jones, 1974

MATERIAL. IOS-7709 # 66: 1 juv. 7709 # 73: 1 ad. ♂, 1 ad. ♀, 1 juv. 7709 # 85: 4 imm. ♀♀. SMBA-ES4: 1 imm. ♂, 1 imm. ♀, 1 juv. ES12: 1 imm. ♂, 3 juv. ES56: 1 ad. ♀. ES59: 1 imm. ♂. ES137: 1 ad. ♀. ES140: 1 imm. ♀. ES147: 1 juv. BIOGAS I-DS09: 1 ad. ♀, 1 imm. ♀. POLYGAS-DS15: 1 ad. ♀. DS16: 1 ad. ♀. BIOGAS II-DS31: 1 imm. ♂, 3 juv. DS32: 1 ad. ♀. BIOGAS III-DS41: 3 ad. ♀♀. BIOGAS IV-DS51: 1 imm. ♀. BIOGAS VI-DS74: 1 ad. ♀. AII60-243: 1 imm. ♂, 1 juv. 246: 5 imm. ♂♂, 8 ad. ♀♀, 22 imm. ♀♀, 50 juv. 256: 2 ad. ♂♂, 3 ad. ♀♀, 1 juv. 259: 1 ad. ♂, 14 imm. ♂♂, 33 ad. ♀♀, 60 imm. ♀♀, 49 juv. 262: 2 ad. ♂♂, 4 ad. ♀♀, 8 imm. ♀♀. 264: 2 imm. ♂♂, 7 juv. Kn25-293: 1 imm. ♂, 1 ad. ♀, 1 juv. 301: 1 ad. ♂, 13 imm. ♂♂, 2 ad. ♀♀, 15 imm. ♀♀. Ch106–323: 1 ad. ♀.

DISTRIBUTION. Described from the Gay Head–Bermuda transect, between 1102 and 3806 m depth, this species is now also recorded from west of Ireland and in Biscay and also from the coasts of Surinam and the Argentine, down to 3917 m.

Campylaspis bacescui Muradian, 1976

MATERIAL. AII60-237: 1 ad. ♀. 239: 1 ad. ♂, 2 ad. ♀♀.

DISTRIBUTION. Recorded by Muradian from off the Argentine, the Falkland Islands and the Straits of Magellan between 82 and 361 m depths, it has now been found off the Argentine coast in greater depths of 1011 to 1679 m.

Campylaspis exarata Jones, 1974

MATERIAL. AII60-245; 9 ad. ♂♂, 17 imm. ♂♂, 65 ad. ♀♀, 7 imm. ♀♀.

DISTRIBUTION. Described from off the coast of tropical Brazil in 587 m depth, it is here recorded from off the Argentine in 2707 m.

Campylaspis mansa Jones, 1974

MATERIAL. IOS-7709 # 72: 3 ad. ♂♂, 1 imm. ♀. 7709 # 73: 2 imm. ♂♂, 5 ad. ♀♀, 2 imm. ♀♀. SMBA-ES4: 7 ad. ♀♀, 1 imm. ♀. ES10: 1 ad. ♂, 3 imm. ♂♂, 1 ad. ♀. ES12: 1 ad. ♂, 5 ad. ♀♀, 7 imm. ♀♀. ES18: 2 imm. ♂♂, 1 imm. ♀. ES27: 1 imm. ♀. ES135: 1 imm. ♀. ES137: 4 imm. ♀♀. ES140: 1 imm. ♀. ES147: 1 imm. ♂, 1 ad. ♀, 7 imm. ♀♀. *Thalassa* 73-Z429: 1 juv. Z442: 1 imm. ♂, 1 ad. ♀, 2 juv. Z447: 2 juv. Z453: 1 imm. ♀. Z459: 1 ad. ♀, 1 imm. ♀, 3 juv. POLYGAS-DS16: 1 imm. ♀. DS20: 1 ad. ♂, 2 ad. ♀♀, 1 juv. DS21: 1 imm. ♂, 1 imm. ♀, 2 juv. DS22: 1 ad. ♂. BIOGAS II-DS31: 2 ad. ♂♂, 6 imm. ♂♂, 7 ad. ♀♀, 3 imm. ♀♀. BIOGAS V-DS66: 3 ad. ♀♀, 6 imm. ♀♀, 1 juv. DS67: 1 ad. ♂, 4 ad. ♀♀, 2 imm. ♀♀. BIOGAS VI-DS76: 1 imm. ♂, 2 imm. ♀♀. DS78: 1 imm. ♂. DS79: 1 imm. ♂, 1 imm. ♀. DS86: 1 ad. ♀. CP23: 1 imm. ♂, 1 ad. ♀, 5 imm. ♀♀. Ch88-209: 1 imm. ♀. Ch106-321: 2 imm. ♀♀. Kn35-340: 1 imm. ♂, 1 imm. ♀, 1 juv.

DISTRIBUTION. Many were found originally on the Gay Head–Bermuda transect between 1135 and 2886 m depth. It is now also recorded from West of Scotland and from Biscay between 975 and 4715 m.

Campylaspis bicarinata Jones, 1974

MATERIAL. BIOGAS III-DS41: 1 ad. ♂, 3 imm. ♂♂, 8 ad. ♀♀, 3 imm. ♀♀. BIOGAS IV-DS55: 2 imm. ♂♂, 2 ad. ♀♀, 2 imm. ♀♀. BIOGAS VI-DS74: 4 imm. ♀♀. AII60-237: 1 ad. ♂, 4 ad. ♀♀. 239: 1 ad. ♂. 243: 1 imm. ♂. 245: 3 ad. ♂♂. 246: 1 ad. ♂. 256: 1 ad. ♂, 3 imm. ♂♂, 1 imm. ♀. Kn25-287: 9 imm. ♂♂, 3 ad. ♀♀ 2 juv. 288: 1 imm. ♀. 291: 1 imm. ♂, 2 juv. 299: 2 imm. ♂♂, 3 imm. ♀♀, 2 juv. 303: 2 ad. ♀♀. Ch106-321: 3 imm. ♂♂, 3 ad. ♀♀, 2 imm. ♀♀, 1 juv. 323: 2 ad. ♂♂, 1 ad. ♀, 1 imm. ♀. 326: 5 imm. ♂♂, 6 ad. ♀♀, 10 imm. ♀♀, 2 juv. 328: 2 imm. ♂♂, 1 imm. ♀, 3 juv.

DISTRIBUTION. Previously recorded from the Gay Head–Bermuda transect and from off tropical Brazil, between 834 and 4680 m, it has now also been found off the Argentine and Surinam and from west of Ireland and Biscay on the eastern side of the North Atlantic down to 5000 m.

Campylaspis propinqua sp. nov.
(Fig. 47)

MATERIAL. Kn25-301: 3 imm. ♂♂, 3 imm. ♀♀.

DESCRIPTION. Immature female, length 4·0 mm: carapace (Fig. 47a, b) about $1\frac{3}{4}$ as long as broad; there is a blunt prominence on either side below the frontal lobe and three pairs of lateral ridges; the upper two ridges on either side run from the antero-lateral angle obliquely upwards to meet dorso-laterally near the hind end of the carapace, forming the boundaries of a depressed area; the third ridge is short and runs parallel to the hind border of the carapace; the pseudorostrum is about $\frac{1}{6}$ of the total carapace length, the lobes gently curved from their meeting point in front, the antero-lateral angle only slightly prominent; the eyelobe is fairly small but broad at the base. Pereon and pleon somites are without spines or serrations.

Antenna 1 (Fig. 47c) with basal segment curved, narrow, little longer than the second segment of the peduncle. Maxilliped 2 (Fig. 47d) with basis fairly broad, carpus broad and propodus long, dactyl with three nearly equal spines much shorter than that of the propodus. Maxilliped 3 (Fig. 47e) with basis broad, its lower distal edge somewhat produced, much shorter than the remaining segments together; the merus widened distally and about as long as the carpus and propodus together. Pereopod 1 (Fig. 47f) with basis broad at its base, a little shorter than the remaining segments together; merus to dactyl successively decreasing a little in length, without spines or serrations. Pereopod 2 (Fig. 47g) with basis about $\frac{3}{5}$ as long as remaining segments together, the carpus about $1\frac{1}{2}$ as long as the merus but only $\frac{3}{5}$ as long as the dactyl, which is tapered but not distally pointed. Uropods (Fig. 47h) with peduncle nearly as long as last three pleonites together, with hyaline serrations on either edge, twice as long as the endopod, which is distinctly longer than the exopod; the endopod has about 5 slender spines on its inner edge and a longer terminal spine.

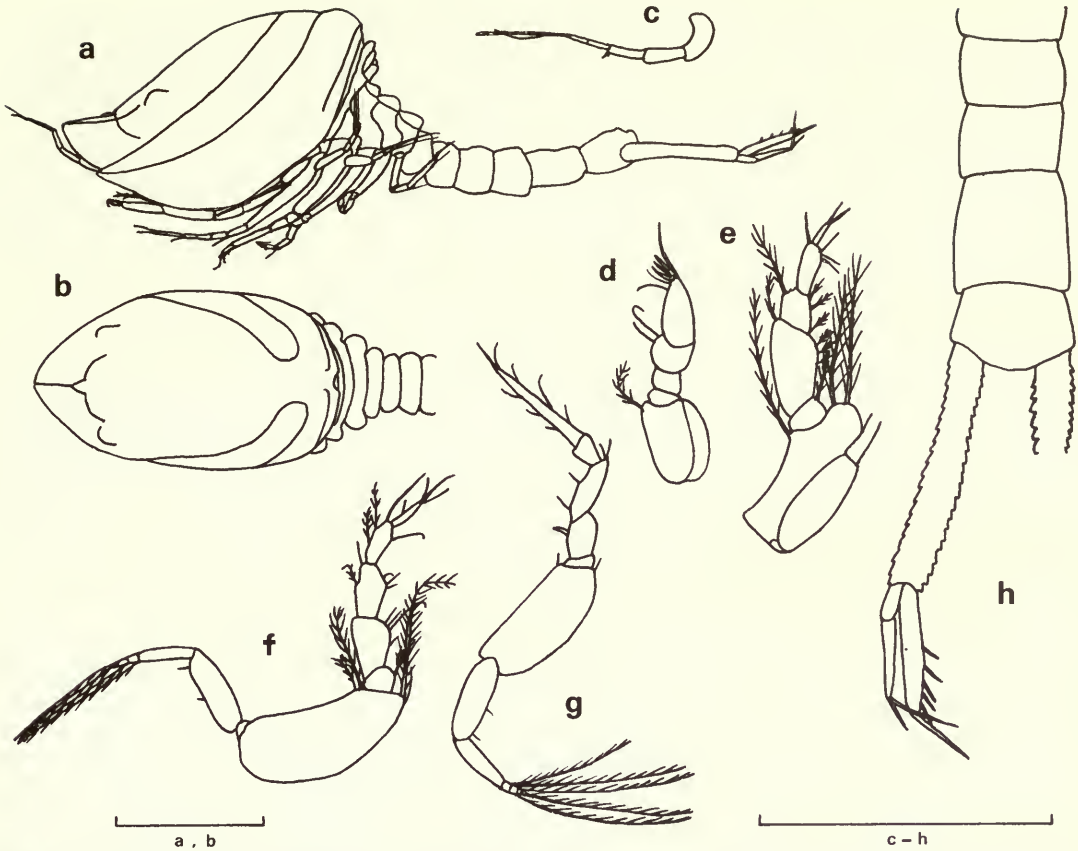

Fig. 47 *Campylaspis propinqua* ♀, (a) lateral view; (b) carapace and pereon from above; (c) antenna 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereopod 1; (g) pereopod 2; (h) uropod and end of pleon.

TYPE LOCALITY. 8° 12.4′ N, 55° 50.2′ W, 2487–2500 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 366 : 1, paratypes 1982 : 367 : 2.

REMARKS. *C. propinqua* resembles *C. bicarinata* but differs in having a third, but short, carina on either side of the carapace, while the two longer carinae meet on either side dorso-laterally to enclose a shallow furrow. The uropods are comparatively shorter and stouter than in *C. bicarinata,* the three dactylar spines of the second maxillipeds are about equal in length, and the bases of the third maxillipeds and first and second pereopods are comparatively short.

DISTRIBUTION. Three immature males and three females were found at a single station off Surinam in 2500 m depth.

Campylaspis rostrata Calman, 1905

MATERIAL. SMBA-SBC67: 1 imm. ♀. *Thalassa* 70-W371: 1 imm. ♀. *Thalassa* 73-Z417: 1 imm. ♀. Z420: 1 imm. ♀. Z428: 1 juv. Z429: 1 juv. Z434: 1 juv. Z439: 1 ad. ♀, 1 imm. ♀. Z442: 1 imm. ♀. Z449: 1 imm. ♀, 1 juv. Z450: 1 juv. BIOGAS II-DS33: 1 imm. ♀. AII59-211: 1 imm. ♀.

DISTRIBUTION. Previous records were from west of Ireland, south-west of the Faroes, the Mediterranean and Biscay, between 220 and 1336 m depth. The further finds recorded here were from west of Scotland, Biscay and the Mediterranean down to 2338 m.

Campylaspis intermedia Hansen, 1920

MATERIAL. POLYGAS-DS26: 1 imm. ♂, 2 imm. ♀♀. BIOGAS III-DS50: 1 imm. ♂, 1 imm. ♀. BIOGAS IV-DS52: 2 ad. ♂♂, 2 imm. ♂♂, 1 ad. ♀, 6 imm. ♀♀, 30 juv. BIOGAS VI-DS86: 1 ad. ♀. DS87: 1 ad. ♀. CP23: 8 imm. ♂♂, 3 ad. ♀♀. 8 imm. ♀♀, 30 juv. CP24: 2 juv. Ch88-207: 2 imm. ♂♂, 8 ad. ♀♀, 6 imm. ♀♀, 12 juv. 209: 1 imm. ♂. Kn35-346: 2 ad. ♂♂, 7 imm. ♂♂, 28 ad. ♀♀, 35 imm. ♀♀, 257 juv.

DISTRIBUTION. First recorded by Hansen from the Davis Strait and south of Jan Mayen, it was later found on the Gay Head–Bermuda transect between 467 and 2178 m depth and also recorded by Muradian-Çiamician (1980) off Beaufort, N.C., from 344 and 692 m. It has now been collected also in Biscay within its previously known depth range.

Campylaspis horrida Sars, 1870

MATERIAL. NORBI-CP11: 1 imm. ♂, 3 ad. ♀♀, 1 imm. ♀, 1 juv.

DISTRIBUTION. Described from the coast of Norway, it was later found south of Iceland and south-west of the Faroes between about 183 and 942 m depth, other records being dubious. The station at which the present record occurred was also from the Norwegian Sea at 300 m and the species seems to be a genuine boreal inhabitant of the upper slope.

Campylaspis tumulifera sp. nov.
(Fig. 48)

MATERIAL. Ch88-207: 3 imm. ♂♂, 3 ad. ♀♀, 1 juv.

DESCRIPTION. Adult female, length 3·9 mm: carapace (Fig. 48a-c) about $1\frac{2}{3}$ as long as deep and $1\frac{3}{4}$ as broad, broadest near the hind end and narrowing in front; the upper half with a number of paired rounded tubercles, several of these forming a short ridge posteriorly on either side; there are shallow excavations behind these ridges and near the antero-lateral angles; most of the body has scattered dark red chromatophores visible through the epidermis; the pseudorostrum is short, about $\frac{1}{8}$ of the total carapace length, obliquely truncated from the side, siphons fairly long; antero-lateral angle well defined and sharp but not prominent, with faint serrations behind it; eyelobe large, sides almost parallel but rounded at front. Anterior pereon somites somewhat raised dorsally. Pereon and pleon without spines and not laterally serrated except faintly on pleonite 5.

Antenna 1 (Fig. 48d) with basal segment broad, nearly as long as subequal second and third together. Maxilliped 2 (Fig. 48e) with basis broadened distally, with a distally thickened seta; the dactyl has three spines, the median small. Maxilliped 3 (Fig. 48f) with basis curved, not narrowed, slightly longer than the remaining segments together, the merus not very broad, none of the segments with spines or serrations. Pereopod 1 (Fig. 48g) with basis somewhat longer than remaining segments together, without serrations. Pereopod (2 (Fig. 48h) with basis broad, not much more than half as long as remaining segments together, the dactyl about $1\frac{1}{2}$ as long as the carpus, slightly tapering. Uropod (Fig. 48i) peduncle with only faint serrations on its basal outer edge, much shorter than last two pleonites together, about $1\frac{1}{2}$ as long as the endopod which has 6 slender spines on its inner edge and a longer terminal spine; it is distinctly longer than the exopod.

TYPE LOCALITY. 39° 51.3′ N–39° 51′ N, 70° 54.3′ W–70° 56.4′ W, 805–811 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 368 : 1, paratypes 1982 : 369 : 3.

REMARKS. This species is similar to *C. paucinodosa* Jones, 1974 and was found in the general area. However, there are several important differences, especially the shape of the basal seta of maxilliped 2, which in *C. paucinodosa* is not thickened, and the relative lengths of the dactyl of pereopod 2, which is shorter than the carpus in *C. paucinodosa.*

DISTRIBUTION. A few specimens of both sexes but including only immature males occurred at a single station south of Gay Head in 805–811 m depth.

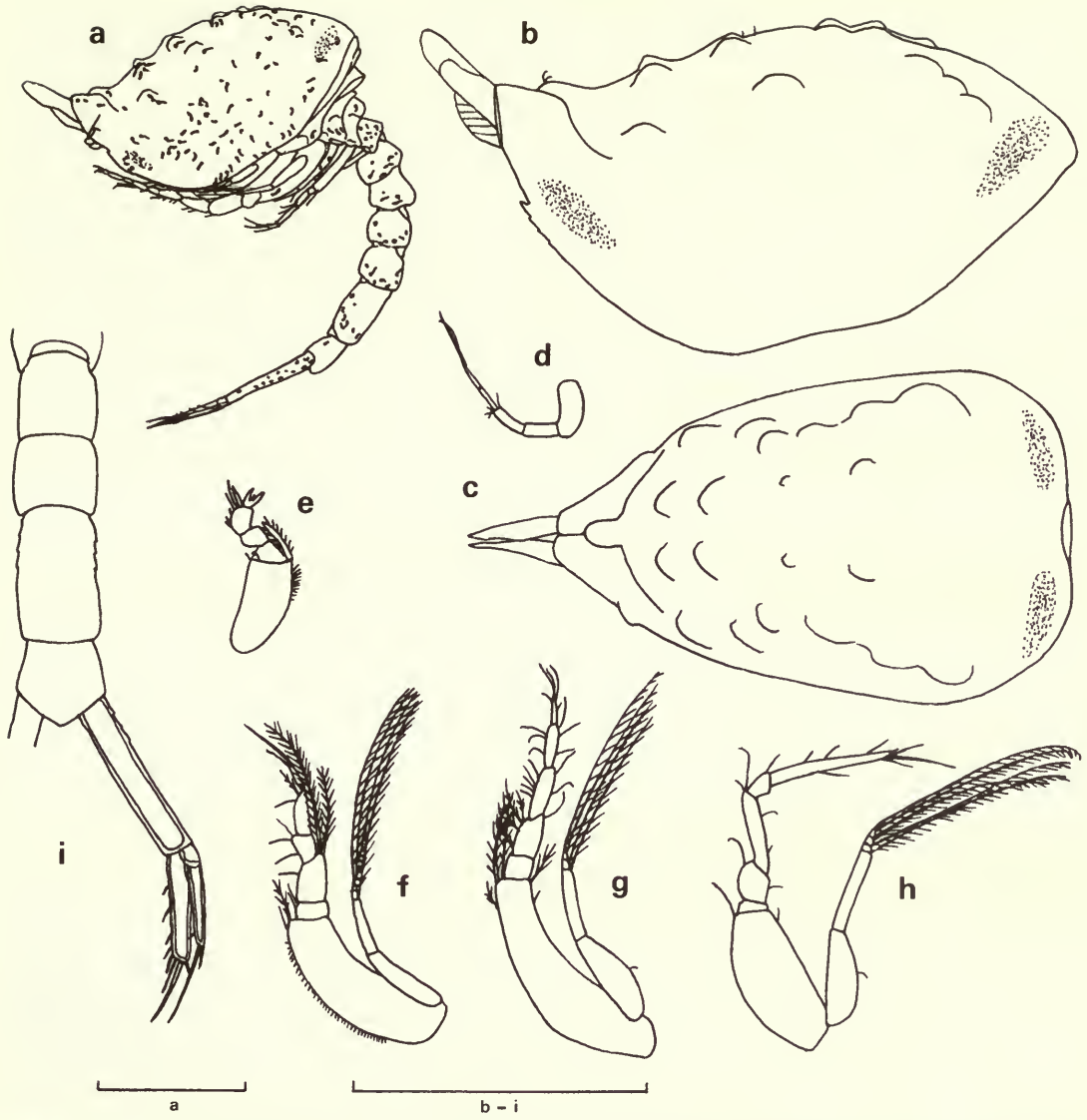

Fig. 48 *Campylaspis tumulifera* ♀, (a) lateral view; (b) carapace from side; (c) carapace from above; (d) antenna 1; (e) maxilliped 2; (f) maxilliped 3; (g) pereopod 1; (h) pereopod 2, (i) uropod and end of pleon.

Campylaspis squamifera Fage, 1929

Campylaspis torulosa Jones, 1974.

MATERIAL. SMBA-ES18: 9 imm. ♂♂, 2 ad. ♀♀, 7 imm. ♀♀. ES20: 6 ad. ♀♀, 7 imm. ♀♀. *Thalassa* 73-Z429: 1 juv. Z443: 1 ad. ♀, 1 imm. ♀. BIOGAS I-DS05; 1 ad. ♀, 1 imm. ♀. DS09: 1 ad. ♂, 14 ad. ♀♀, 2 imm. ♀♀. DS11: 1 ad. ♀. DS12: 1 imm. ♀. DS13: 1 imm. ♂, 17 ad. ♀♀, 2 juv. POLYGAS-DS15: 4 imm. ♂♂, 5 ad. ♀♀, 8 imm. ♀♀, 19 juv. DS16: 1 imm. ♀, 10 juv. DS17: 2 ad. ♀♀, 2 imm. ♀♀, 4 juv. DS18: 6 imm. ♂♂, 25 ad. ♀♀, 34 imm. ♀♀. DS20: 1 imm. ♂. DS21: 1 imm. ♀. BIOGAS III-DS35: 6 ad. ♀♀, 2 imm. ♀♀, 3 juv. DS36: 2 imm. ♀♀. DS38: 3 ad. ♀♀, 2 imm. ♀♀. BIOGAS IV-DS62: 3 imm. ♂♂, 4 imm. ♀♀. DS63: 3 imm. ♀♀. DS64: 1 imm. ♂. BIOGAS V-DS65: 2 imm. ♀♀. DS67: 1 imm. ♂. BIOGAS VI-DS76: 2 imm. ♂♂, 2 imm. ♀♀. CP09: 3 mm. ♀♀. Ch106-326: 4 imm. ♂♂, 7 ad. ♀♀, 5 imm. ♀♀, 15 juv. Kn35-346: 1 imm. ♂.

REMARKS. I have now concluded that *C. squamifera* and *C. torulosa* are identical and that any apparent difference was due to the immaturity of the single male on which Fage's description was based.

DISTRIBUTION. *C. squamifera* was first recorded from the Bay of Biscay at 4380 m depth and later between 641 and 860 m. The present records are from many stations in Biscay and some west of Ireland and also on the Gay Head–Bermuda transect between 457 and 4228 m. *C. torulosa* was found on the Gay Head–Bermuda transect between 4680 and 4825 m and later reported by Muradian-Çiamician (1980) off Beaufort, N.C., and southern Greenland between 274 and 344 m. Muradian-Çiamician (1980) suggested that a new description of *C. squamifera* would be opportune.

Campylaspis horridoides Stephensen, 1915

MATERIAL. *Thalassa* 73-Z435: 1 imm. ♂. Z437: 1 imm. ♀. BIOGAS II-DS33: 3 imm. ♂♂, 4 ad. ♀♀, 2 imm. ♀♀. DS34: 2 ad. ♂♂. AII59-211: 5 ad. ♂♂, 1 imm. ♂, 26 ad. ♀♀, 20 imm. ♀♀. 214: 1 imm. ♀.

DISTRIBUTION. Previous records were from the Mediterranean and Biscay between 843 and 2447 m depth. The records reported here were from the same areas but the minimum depth is raised to 509 m.

Campylaspis frigida Hansen, 1908

MATERIAL. AII60-237: 49 imm. ♂♂, 2 ad. ♀♀, 83 imm. ♀♀, 47 juv. 239: 5 imm. ♂♂, 11 ad. ♀♀, 31 imm. ♀♀. 240: 2 imm. ♀♀. 245: 3 imm. ♂♂, 1 ad. ♀, 4 imm. ♀♀.

DISTRIBUTION. Described from the Antarctic and subsequently recorded from Kerguelen (Ledoyer, 1977), Muradian-Çiamician (1980) also recorded many specimens from the southern tip of South America and from the Argentine continental shelf between 24 and 3845 m depth. The finds reported here were off the Argentine coast between 1011 and 2707 m.

Campylaspis verrucosa Sars, 1866

MATERIAL. SMBA-ES15: 6 imm. ♂♂, 5 ad, ♀♀, 17 imm. ♀♀, 6 juv. ES18: 1 ad. ♀. *Thalassa* 70-W357: 7 ad. ♂♂, 3 imm. ♂♂, 5 ad. ♀♀, 6 juv. *Thalassa* 72-Y374: 2 juv. *Thalassa* 73-Z399: 1 juv. Z414: 2 imm. ♀♀. Z439: 1 imm. ♀. Z449: 1 imm. ♀. POLYGAS-DS26: 2 ad. ♂♂, 4 imm. ♂♂, 11 ad. ♀♀, 4 imm. ♀♀, 1 juv. BIOGAS III-DS49: 2 ad. ♀♀, 3 imm. ♀♀. DS50: 1 imm. ♂, 2 ad. ♀♀, 2 imm. ♀♀. BIOGAS IV-DS51: 3 ad. ♀♀, 2 imm. ♀♀. DS52: 2 ad. ♀♀, 4 imm. ♀♀, 1 juv. DS55: 1 imm. ♂, 2 imm. ♀♀, 7 juv. BIOGAS VI-DS86: 2 imm. ♂♂, 2 ad. ♀♀, 21 imm. ♀♀, 14 juv. DS87: 1 ad. ♂, 7 ad. ♀♀, 11 imm. ♀♀, 10 juv. DS88: 1 juv. CP23: 1 imm. ♂, 2 imm. ♀♀, 3 juv. CP24: 2 imm. ♂♂, 1 ad. ♀, 1 juv. CP25: 1 imm. ♂, 5 juv. Ch106-313: 1 imm. ♂, 16 ad. ♀♀, 41 imm. ♀♀. 321: 1 imm. ♂.

DISTRIBUTION. Previously recorded from off Norway to the coast of Portugal and from the Mediterranean between 100 and 1739 m depth, it is now also recorded from Biscay and west of Scotland and south of Gay Head down to 4125 m.

Campylaspis globosa Hansen, 1920

MATERIAL. IOS-7709 # 62: 2 ad. ♀♀. 7709 # 66: 1 ad. ♀. 7709 # 72: 1 imm. ♀. 7709 # 73: 6 ad. ♀♀, 4 juv. 7709 # 85: 4 ad. ♀♀. SMBA-ES4: 4 imm. ♂♂, 2 ad. ♀♀, 10 imm. ♀♀. ES12: 9 imm. ♂♂, 2 ad. ♀♀, 6 imm. ♀♀, 13 juv. BIOGAS I-DS09: 1 ad. ♂, 2 ad. ♀♀, 1 juv. DS13: 10 ad. ♀♀, 1 imm. ♀. POLYGAS-DS15: 1 ad. ♂, 3 imm. ♂♂, 1 imm. ♀, 1 juv. DS18: 2 ad. ♂♂, 5 imm. ♂♂, 5 ad. ♀♀, 18 imm. ♀♀. DS25: 1 ad. ♀, 1 juv. DS28: 1 ad. ♀. BIOGAS II-DS31: 1 ad. ♂, 4 imm. ♂♂, 18 ad. ♀♀, 17 imm. ♀♀, 3 juv. DS32: 1 ad. ♀. DS33: 1 imm. ♂, 1 imm. ♀. BIOGAS III-DS35: 2 imm. ♀♀, 1 juv. DS36: 1 ad. ♀. DS38: 1 imm. ♀. DS41: 1 imm. ♂, 3 ad. ♀♀, 1 imm. ♀, 2 juv. BIOGAS IV-DS51: 1 imm. ♂, 3 ad. ♀♀, 4 imm. ♀♀, 4 juv. DS62: 1 imm. ♂. DS63: 1 ad. ♀, 2 imm. ♀♀, 1 juv. BIOGAS VI-DS74: 1 imm. ♂, 6 imm. ♀♀, 1 juv. CP09: 1 imm. ♀. NORBI-CP11: 1 imm. ♀. Ch88-207: 1 imm. ♂, 3 ad. ♀♀, 4 imm. ♀♀. Kn25–299: 4 imm. ♂♂, 3 ad. ♀♀, 10 imm. ♀♀. Kn35-346: 2 ad. ♂♂, 8 imm. ♂♂, 5 ad. ♀♀, 8 imm. ♀♀, 2 juv.

DISTRIBUTION. First described from the Davis Strait and subsequently from the Gay Head–Bermuda transect between 498 and 2886 m depth, it was also reported by Muradian-Çiamician (1980) off Beaufort. N.C., between 334 and 2030 m. It is now recorded from many stations in Biscay and also from off Norway, west of Ireland and from one station off Surinam and its depth range extended to between 300 and 4413 m.

Campylaspis nodulosa Sars, 1887

MATERIAL. AII60-240: 1 imm. ♀. 245: 3 imm. ♀♀. 246: 8 imm. ♂♂, 2 ad. ♀♀, 22 imm. ♀♀. 247: 2 imm. ♂♂.

DISTRIBUTION. Described from the Antarctic and recorded from Kerguelen (Ledoyer, 1977) and also by Muradian-Çiamician (1980) from the Argentine shelf and slope, between 64 and 1475 m depth, it is now recorded from deeper water off the Argentine, between 2323 and 5233 m.

Campylaspis multinodosa Jones, 1974

MATERIAL. AII60-259: 34 imm. ♂♂, 1 ad. ♀, 31 imm. ♀♀.

DISTRIBUTION. Described from off South-west Africa between 1007 and 2154 m depth, it is now recorded from a single station off the Argentine coast in 3317 m.

Genus *PARACAMPYLASPIS* nov.

Generally resembling *Campylaspis* but antero-lateral angles of carapace well produced; maxilliped 2 with ischium distinct and propodus drawn out into a long flexible process reach-

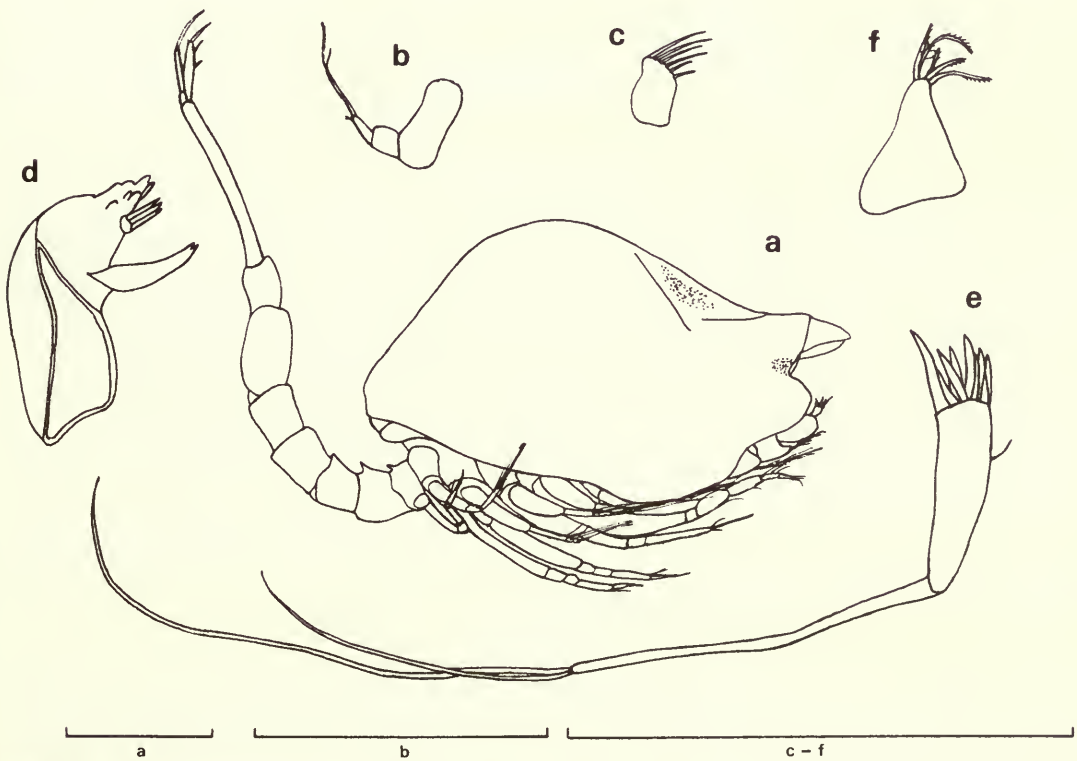

Fig. 49 *Paracampylaspis platycarpus* ♀, (a) lateral view; (b) antenna 1; (c) labium; (d) mandible; (e) maxilla 1; (f) maxilla 2.

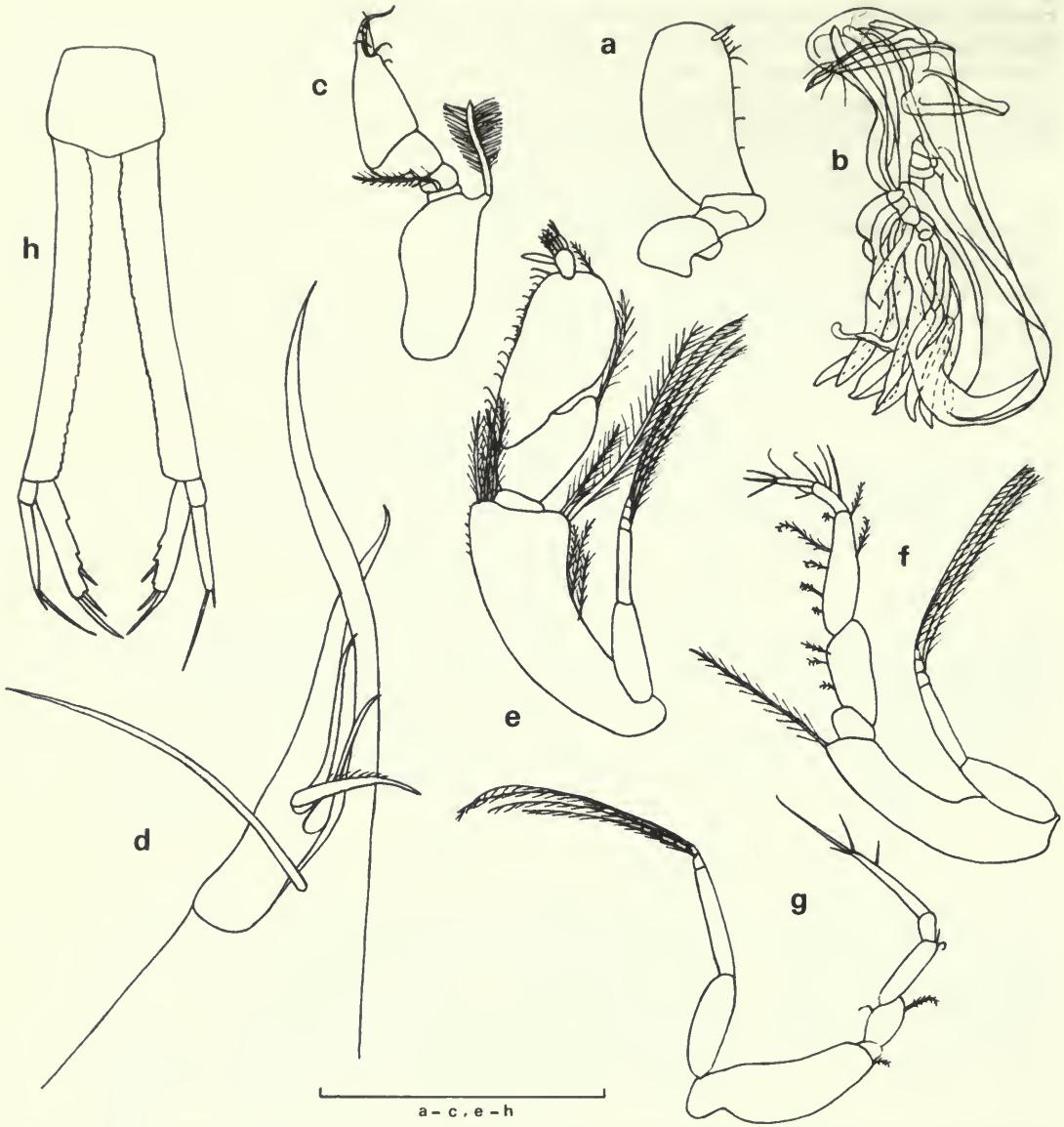

Fig. 50 *Paracampylaspis platycarpus* ♀, (a) maxilliped 1; (b) branchial part of maxilliped 1; (c) maxilliped 2; (d) distal part of maxilliped 2 (further enlarged); (e) maxilliped 3; (f) pereopod 1; (g) pereopod 2; (h) uropods and end of pleon.

ing well beyond the end of the dactyl and maxilliped 3 with carpus much expanded, forming with its fellow a valve covering the mouthparts.

Paracampylaspis platycarpus sp. nov.
(Figs. 49, 50)

MATERIAL. IOS-6696: 2 ad. ♀♀. SMBA-ES20: 1 ad. ♂. *Thalassa* 73-Z429: 1 ad. ♀, 1 juv. Z447: 1 ad. ♀.

DESCRIPTION. Adult female, length 5·1 mm: carapace (Fig. 49a) strongly domed dorsally and overlapping the first three pereon somites, without spines or serrations; antennal notch

excavated and antero-lateral angle well produced but rounded; eyelobe rudimentary. Last pereonite and first two pleonites with dorsal backward-pointing projections.

Antenna 1 (Fig. 49b) with segments rather stout, the basal longer than the second and third together. Mandibles (Fig. 49d) with molar process styliform as in *Campylaspis.* Maxilla 1 (Fig. 49e) with two palps. Maxilla 2 (Fig. 49f) a single plate without endites. Maxilliped 1 (Fig. 50a, b) similar to that of *Campylaspis;* branchial part with about 15 leaflets and two accessory lobules. Maxilliped 2 (Fig. 50c, d) with the ischium distinctly separated; the terminal seta on the basis is thickened and heavily plumose; the propodus is broad at the base and elongated, ending in a long flexible process; the dactyl is articulated inside the base of this process and is also elongated and flexible, bearing several setae, but is much shorter than the propodal process. Maxilliped 3 (Fig. 50e) with basis stout, widest distally, shorter than remaining segments together; the merus is broad and expanded outwards and the carpus much expanded; the propodus is short and has a stout spine on the inner edge; the dactyl is narrow and small. In pereopod 1 (Fig. 50f) the basis is shorter than the remainder of the appendage; the merus and carpus are fairly broad; the propodus and dactyl are subequal and narrower, together about $\frac{2}{3}$ as long as the carpus. In pereopod 2 (Fig. 50g) the dactyl is moderately tapered, about three times as long as the propodus and distinctly longer than the carpus. The uropods (Fig. 50h) long, about as long as the last four pleonites combined; bases serrated on the inner edge, nearly three times as long as the endopod, which is also serrated on its inner edge and has three spines; the exopod is narrower and somewhat shorter.

Adult male, length 5·7 mm: generally similar in shape to female. Dorsal projections on last pereonites and anterior pleonites with bunches of hooked setae. Second antennal flagellum reaching beyond hind end of pleon.

TYPE LOCALITY. 28° 06′ N. 13° 28′ W, 1780 m. Type specimens deposited in the British Museum (Natural History). Holotype 1982 : 370 : 1, allotype 1982 : 371 : 1, paratype 1982 : 372 : 1.

DISTRIBUTION. Recorded from the Canary Islands, the Bay of Biscay and west of Scotland, 1271 to 1780 m depth.

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The material from the Station Biologique de Roscoff and the Centre Océanologique de Bretagne has been sorted by the Centre National de Tri d'Océanographie Biologique and I am indebted for it to M M. Segonzac.

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On the foraminiferal genera *Tritaxis* Schubert and *Trochamminella* Cushman (Protozoa: Foraminiferida)

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I. On *Tritaxis* Schubert

The name *Tritaxis* was coined by Schubert (1920: 180) for triserial agglutinated post-Palaeozoic foraminifera which he considered to be the descendants of *Tetrataxis* Ehrenberg. Schubert expressed his reasoning as follows:

> . . . die palaeontologisch primitiveren Formen *Globivalvulina* und *Tetrataxis* dagegen wandeln sich im Mesozoicum um: erstere in manche Globigerinen [*sic*] und von letzterer die einfachen Typen (z.B. die ohne extrem ausgebildete Nabelhöhlung) durch stärkere Sarkodenzunahme zunächst zu Formen, bei denen nicht vier, sondern nur drei Kammern einen Umgang aufbauen. Die letztere Verhältnis scheint nun für eine grössere Reihe von Formen konstant geworden zu sein, besonders für die postpalaeozoischen und jüngsten sogar noch lebenden Vertreter (*Fusca* Will., *conica* P. u J.) die sich durch den Mangel einer zentralen Höhlung auch nicht unwesentlich von den karbonen Valvulinen, den *Tetrataxis*arten, unterscheiden; *deshalb scheint sich auch ihre (etwa subgenerische) Abgrenzung von den karbonen etwa als Tritaxis zu empfehlen* [our italics].

Tritaxis, born therefore in the course of speculations into the evolution of agglutinated foraminifera, was formalised taxonomically by Cushman (1928) who designated as its type species *Rotalina fusca* Williamson, a trochamminid foraminifer from the Recent of the British Isles (Williamson, 1858: 55, pl. 5, figs 114, 115). Now a genus within the Trochamminidae Schwager, it was however immediately placed by Cushman (1928: 171) into synonymy with *Trochammina* Parker & Jones (type species: *Nautilus inflatus* Montagu, 1808, from the Recent of SW England). Cushman (1948: 202) subsequently did not change this opinion and listed, in the fourth edition of his *Foraminifera. Their classification and economic use, Tritaxis* as a synonym of *Trochammina.* This was also accepted by Bermúdez & de Rivero (1963). Glaessner (1945: 99) considered *Tritaxis* as a separate subgenus of *Trochammina* characterised by a low, conical test, and included within it Jurassic and Recent species (see discussion in Bermúdez & de Rivero, 1963: 318).

It was Loeblich & Tappan (1955: 19) who reinstated *Tritaxis* as a valid genus. They amended it to include low trochoid trochamminid tests with at first 4 chambers per whorl, then only 3 in the final whorl; free-living in early ontogeny and attached in the adult stage, with an areal ovate aperture in the free-living forms and a tubular aperture in the attached. These authors stated that . . . 'the types of Williamson's species are missing from the British Museum Collections', and based their emended definition of *Tritaxis* on specimens labelled *Tritaxis fusca* (Williamson) encountered in the F.C. *Helga* haul no. SR 331 from off SW Ireland, depth 610–680 fathoms (1115–1245 m), deposited in the collections of the United States National Museum (USNM), reg. nos P 2198a, b. The two hypotypes illustrated by Loeblich & Tappan (1955: pl. 3, figs 5a–c, 6) have been examined by one of us (P.B.) who

reports that their drawings are indeed accurate representations. The non-attached individual shown in pl. 3, figs 5a–c, has spirally 4 subglobular chambers in the early, and 3 elongate crescentic chambers in the final whorl. Umbilically, the 3 final chambers are flattened and an oval areal aperture occurs close to the base of the septum of the final chamber over the first chamber of the last whorl as Loeblich & Tappan indeed state. These authors considered the attached form (1955: pl. 3, fig. 6) as conspecific. It has the same morphology as the free specimen, with 4 subglobular early chambers and 3 elongate crescentic ones in the final whorl. Around the margins, the test is surrounded by a spongy calcareous mass, with a very few agglutinated grains of irregular outline but devoid of any tunnel-like extensions as developed in *Trochamminella siphonifera* Cushman (1943: 95, pl. 16, figs 18–20). The attached and free specimens are from the same sample and in view of their morphological similarity, Loeblich & Tappan's assumption that they are conspecific, seems to us a reasonable one. In the same paper, Loeblich & Tappan illustrate (1955: pl. 3, fig. 7) the holotype of *Trochamminella siphonifera* Cushman, housed in the USNM reg. no. 39619, from Johnson-Smithsonian Expedition station 25, off Puerto Rico (depth 240–300 fathoms/440–550 m). Brönnimann has also examined this specimen and again can verify that both Cushman's original illustration (1943, pl. 16, fig. 18) and that of Loeblich & Tappan, are accurate. *Trochamminella* is however placed in synonymy with *Tritaxis* by Loeblich & Tappan (1955: 20), a conclusion they also follow in the *Treatise of Invertebrate Paleontology* (Loeblich & Tappan, 1964: C266).

Taxonomically important in Loeblich & Tappan's revision are the following two points:

(1) They did not establish a neotype for *Tritaxis fusca* (Williamson). They based their emended definition of *Tritaxis* on hypotypic specimens considered to represent *T. fusca,* collected in deepwater off SW Ireland, not one of the localities listed by Williamson (1858).

(2) The synonymising of *Trochamminella* with *Tritaxis* is based on the comparison of these above mentioned specimens of *T. fusca* with the holotype of *Trochamminella siphonifera.*

Hedley *et al.* (1964), in the course of a larger study of New Zealand intertidal foraminifera, re-examined the case of *Tritaxis fusca* (Williamson) on the basis of material deposited in the British Museum (Natural History). Hedley *et al.* reiterate Loeblich & Tappan's (1955) statement that the type specimen is missing from the Williamson Collection. They do however figure ... 'a specimen removed by the authors from material donated by H. B. Brady to W. C. Williamson'; it is from shore sand, Isle of Skye, and is one of the localities listed by Williamson in his original description. This specimen was illustrated by a drawing in Hedley *et al.*'s paper as their fig. 2: 1A–C and described as follows (ex tabulation, pp. 420, 421):

> Test free, trochoid, concavo–convex, maximum diameter 250 μm, [axial] height 130 μm. Spirally low trochoid; umbilically excavated; outline circular. Early chambers nearly globular, later ones crescentric: 16 chambers arranged in 4 whorls with 3 chambers in the final whorl; the final chamber occupies about half of the umbilical side. Sutures distinct, slightly depressed, curved slightly backwards on spiral side and straight on umbilical side. Aperture distinct, at the inner margin of umbilical side of the last chamber, extraumbilical. Wall finely arenaceous with occasional larger grains, smoothly finished. Colour golden brown, last chamber almost white.

We have re-illustrated this specimen by Scanning Electron Microscopy (Figs 11–14). The specimen was found to be damaged prior to scanning, but nevertheless it is clear that Hedley *et al.*'s description agrees well with our photographs, except that a small portion of a fourth chamber is shown umbilically. There are, however, several differences between this specimen and that of Williamson (1858: 55, figs 114, 115) which warrant our attention. Williamson's specimen consists of 11 chambers, 3 in the final whorl, while, umbilically, the ultimate chamber makes up about half the test. In Hedley *et al.*'s specimen, on the other hand, there are 16 chambers on the spiral side, with 4 in the final whorl, and umbilically the final

chamber makes up less than half the test. Furthermore, the latter is barely half the size of the original specimen.

Nevertheless, in spite of these difficulties Hedley *et al.*'s paper (1964) contains several salient taxonomic points:

(1) It was confirmed that the type of *Rotalina fusca* is missing from the extant part of the Williamson Collection in the BM(NH).
(2) They did not establish a neotype.
(3) They showed that a specimen from one of Williamson's original localities, which they considered to represent *fusca,* existed in material in the Brady Collection (BM(NH)), having been donated by Williamson himself. They demonstrated that this trochamminid was completely different in apertural features to *Tritaxis fusca sensu* Loeblich & Tappan (1955; 1964).

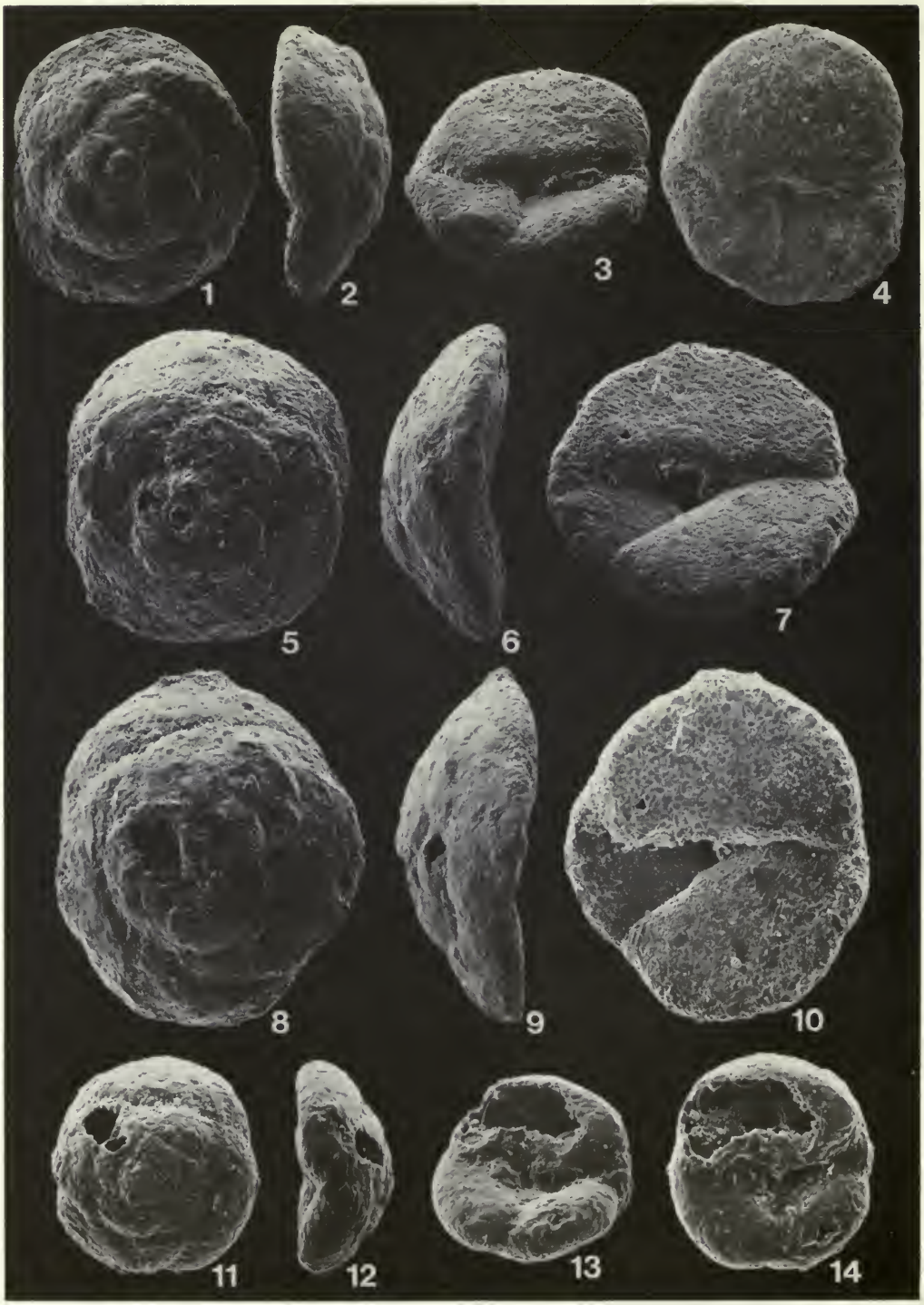
We now have differing concepts of *Tritaxis fusca.* One, the *fusca* of Loeblich & Tappan, based on material from off SW Ireland, with a single areal aperture, and *fusca* of Hedley *et al.* from Williamson's material, Isle of Skye, with a single interiomarginal aperture which rests with its border completely on the first chamber of the final whorl in an extraumbilical position. It will be shown that the former is referable to *Trochamminella* whereas the latter is correctly assigned to *Tritaxis.*

Because of our misgivings, outlined above, as to whether Hedley *et al.*'s (1964) specimen is conspecific with the true *fusca,* we initiated a further search for Williamson's type specimen. There is however a gap in the registered numbers of the Williamson Collection and it is indeed probable that the slide containing the specimen representing his figs 114, 115, was never presented in the first place; it must therefore be presumed lost. In the course of this search for the type, one of us (J.E.W.) encountered more material in the Brady Collection of the BM(NH) from 'deepwater off the Isle of Skye', donated by Williamson. This apparently belonged to the same suite of material in which Hedley *et al.* found the single specimen which they figured in 1964. Their material was however labelled 'shore sand, Skye', not 'deepwater, off the Isle of Skye', as is ours. Williamson (1858: 56) merely states under his localities . . . 'Skye (not uncommon), . . .' and therefore it is reasonable to assume that both samples were known to him when he made the description. We do not however know the locality from which his figured specimen came, while no syntypic material from the other five localities is extant. Instead of the sole specimen found by Hedley *et al.* and which they referred to *T. fusca* (we have re-picked the sample and there are no more), we have found a large suite of specimens in the latter sample which fit better Williamson's original description and figure. They all have 3 chambers in the final whorl (the last chamber being about half the size of the test), 11 or 12 chambers on the spiral side and a test diameter (400–650 μm) more in keeping with Williamson's dimensions (1/60th of an inch or c. 450 μm). The aperture is interiomarginal.

As there is obviously still confusion over what *fusca* and its genus, *Tritaxis,* really are, a neotype should now be established in order to stabilise the nomenclature. From the 'deepwater off the Isle of Skye' residue we have picked out several specimens to show the variation within the species (Figs 1–4; 5, 6; 7–10) and here select specimen ZF 4209 as neotype of *Rotalina fusca* Williamson. It is very similar to Williamson's original figures, particularly in umbilical view, and for the reasons already stated it is preferable as neotype to the specimen described by Hedley *et al.* (1964).

Tritaxis fusca (Williamson), 1858
Figs 1–10; ?11–14; 19–27

NEOTYPE. ZF 4209, from off the Isle of Skye, NW Scotland; deep water. From material donated by W. C. Williamson to H. B. Brady, ex Brady Collection, BM(NH). Figured by Scanning Electron Microscopy in Figs 1–4.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PARANEOTYPES. ZF 4208 (Figs 1–4) and ZF 4210 (Figs 5, 6), both from same sample as neotype. 5 other free specimens were picked out for comparative purposes but they are not formally designated paraneotypes. A further single attached specimen was also found in the same sample which is assumed to be conspecific; the extreme fragility of the test, however, precluded its removal for cleaning and analysis of the aperture (see p. 298, below).

OTHER SPECIMENS. 5 attached specimens from *Terra Nova* station 96 (Heron-Allen & Earland station 6), 7 miles E of North Cape, New Zealand (long. 173°04′E, lat. 34°23′S), depth 70 fathoms (128 m), ex Heron-Allen & Earland type slide 282 (material 96D), collected 3rd August 1911. Labelled in their faunal-slide collection notes as '*Valvulina fusca* (Williamson)'. ZF 4201, 4202 (both unfigured); 4203 (Figs 25–27, attached; Figs 19–22, subsequently removed from its attachment); 4206 (unfigured); 4207 (Figs 23, 24).

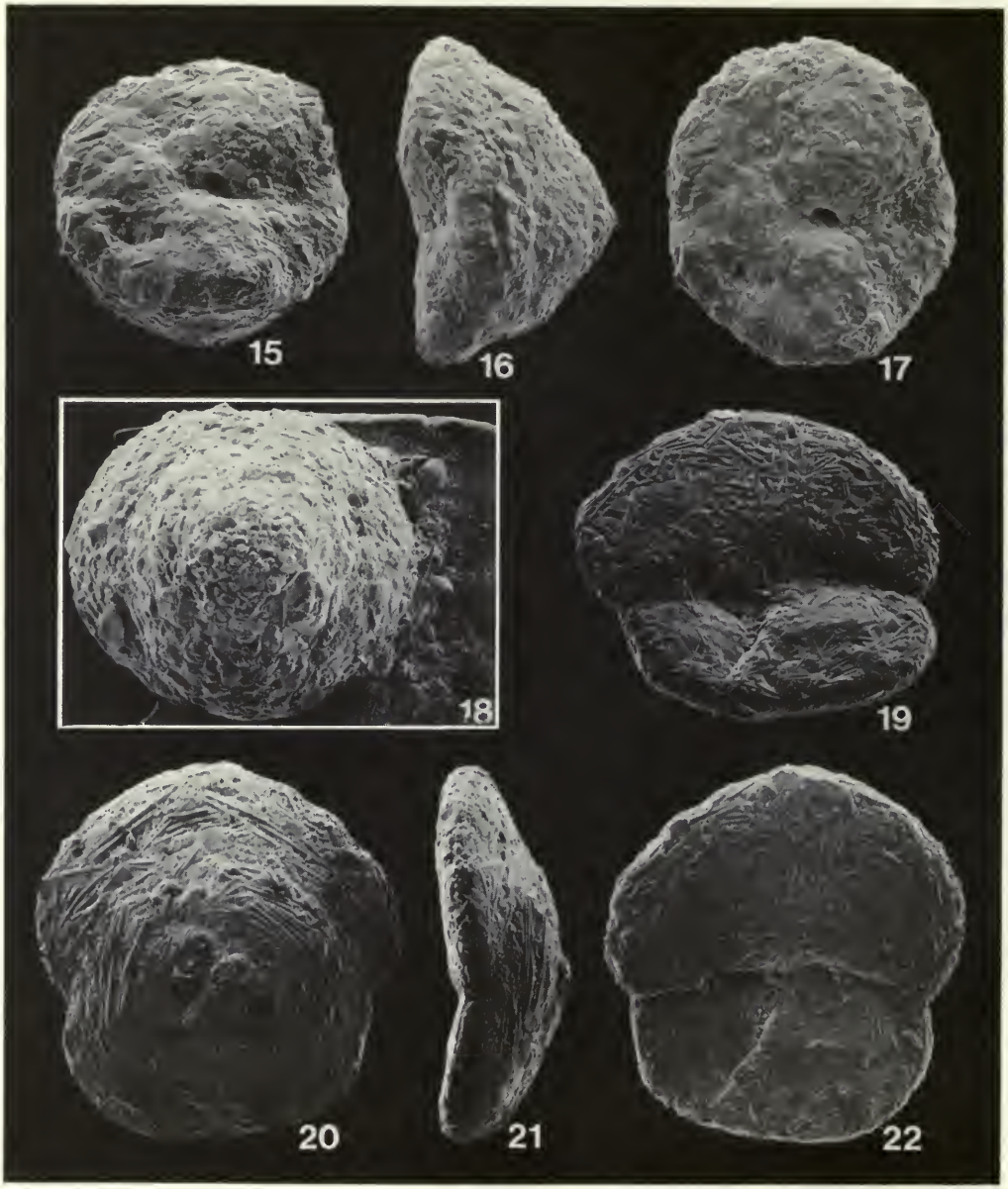
DESCRIPTION (NEOTYPE). Test free, low dextral trochospire; domed-convex spirally, shallow-concave umbilically; subcircular in outline in spiral and umbilical view; compressed-rounded periphery in edge view. Spirally with 11 chambers, including proloculus, arranged in about 2 whorls. Early chambers subglobular, those of 3-chambered final whorl strongly compressed axially, elongate-crescentic on spiral side, flattened on umbilical side; final chamber occupies about half of umbilical side, penultimate chamber, which is in part overlapped by the ultimate, occupies more than one-third, and first chamber of final whorl occupies about one-sixth. Umbilical (axial) depression small and deep, almost closed. Sutures distinct both umbilically and spirally, except over initial part of test. Aperture single, interiomarginal, a slightly obliquely arranged slit, with border resting completely on surface of first chamber of final whorl, extraumbilical and of *Trochammina*-type, with thin protruding rim. Wall agglutinated, fragile, apparently single-layered, imperforate. Agglutinant of larger scale-like rock fragments on spiral side, with smaller fragments umbilically.

DIMENSIONS (NEOTYPE). Maximum spiral and umbilical diameter 600 μm, minimum diameter 520 μm, axial height (thickness) 230 μm.

VARIATION (PARANEOTYPES). ZF 4210 is illustrated by spiral and edge views in Figs 5, 6. It is a sinistral specimen with 11 crescentic elongate chambers (including the proloculus) on the spiral side and 3 chambers, of the same proportions as found in the neotype, on the umbilical side. The umbilicus is narrow and deep and the aperture is also as seen in the neotype (the umbilical view is not shown because of a badly damaged final chamber). ZF 4208 (Figs 1–4), although a dextral specimen, has also 11 chambers in total on the spiral side. The 3 umbilical chambers, however, are of different proportions to that seen in the neotype and the aperture is a low-elongate interiomarginal slit parallel to the suture, but still of *Trochammina*-type and accompanied by a distinctly protruding lip which is discernible even in normal umbilical view (Fig. 4). Several other individuals from the type locality have an aperture of this kind, rather than the obliquely arranged aperture of the neotype and specimen ZF 4210, which cannot be readily seen without tilting the specimen and no doubt led Williamson (1858: 55) to describe the aperture as 'indistinct'.

Figs 1–10 *Tritaxis fusca* (Williamson). Figs 1–4, Paraneotype (ZF 4208). Spiral, edge, oblique-umbilical and umbilical views. Figs 5, 6, Paraneotype (ZF 4210). Spiral and edge view. Figs 7–10, Neotype (ZF 4209). Oblique-umbilical, spiral, edge and umbilical views. All ×88. All from Skye, NW Scotland. From material donated by Williamson to Brady; ex Brady Collection, BM(NH). Material labelled 'deep water'.

Figs 11–14 *Tritaxis* sp. 1963.2.19.17. Spiral, edge, oblique-umbilical and umbilical views. ×125. Identified by Hedley *et al.* (1964) as *T. fusca* (Williamson) and figured (drawing) in figs 2: 1A–C. From Skye, NW Scotland. From material donated by Williamson to Brady; ex Brady Collection, BM(NH). Material labelled 'shore sand'.



Figs 15–18 *Tritaxis australis* Brönnimann & Whittaker sp. nov. Figs 15–17, Holotype (ZF 4204). Oblique-umbilical, edge and umbilical views. Fig. 18, Paratype (ZF 4205). Spiral view of attached specimen. Both ×88. Both from *Terra Nova* station 96 (Heron-Allen & Earland station 6), 7 miles E of North Cape, New Zealand, depth 70 fathoms (128 m), ex Heron-Allen & Earland Collection, BM(NH).

Figs 19–22 *Tritaxis fusca* (Williamson). ZF 4203. Oblique-umbilical, spiral, edge and umbilical views of formerly attached specimen (see Figs 25–27). ×88. From *Terra Nova* station 96 (Heron-Allen & Earland station 6), 7 miles E of North Cape, New Zealand, depth 70 fathoms (128 m), ex Heron-Allen & Earland Collection, BM(NH).

Figs 23–27 *Tritaxis fusca* (Williamson). Figs 23, 24, ZF 4207. Spiral view of attached specimen; detail of wall and part of surrounding 'spongy calcareous' mass, ×88 and ×220, respectively. Figs 25–27, ZF 4203. Spiral view of attached specimen, since removed (see Figs 19–22); detail of wall and parts of surrounding 'spongy calcareous' mass: fig. 25, ×88; figs 26, 27, ×115 and ×130, respectively. Both from *Terra Nova* station 96 (Heron-Allen & Earland station 6), 7 miles E of North Cape, New Zealand, depth 70 fathoms (128 m), ex Heron-Allen & Earland Collection, BM(NH).

DIMENSIONS(PARANEOTYPES)

	Umbilical and spiral diameter		Axial height
Specimen (Figs)	Maximum	Minimum	(thickness)
ZF 4208 (Figs 1–4)	460 μm	410 μm	170 μm
ZF 4210 (Figs 5, 6)	520 μm	450 μm	210 μm

REMARKS. As the neotype of *T. fusca* is characterised by an interiomarginal *Trochammina*-type aperture, the forms described by Loeblich & Tappan (1955: 19, pl. 3, figs 5a–c, 6) with areal apertures are not conspecific and should be placed in *Trochamminella siphonifera* Cushman. *Tritaxis* is now emended to coincide with our redescription of the type-species with added observations based on attached material and a new species, previously identified as *fusca,* both from the *Terra Nova* Collection, off New Zealand.

In the Skye material there was only one attached individual and its fragility precluded its removal from its shell fragment and observation of the umbilical side. Instead, 5 attached specimens from *Terra Nova* station 96, 7 miles E of North Cape, New Zealand, which we

consider conspecific with *T. fusca,* were examined. Of these, two specimens, ZF 4203 and ZF 4207, are illustrated in Figs 19–22, 25–27, and Figs 23, 24, respectively. In its attached state (Figs 25–27), the test of the former is surrounded and glued to a bivalve fragment by a granular spongy calcareous secreted material in which some foreign elements are embedded. Subsequently removed and cleaned it is illustrated in its free state in Figs 19–22. It is a dextral low trochospire of 11 chambers (including the proloculus) and in umbilical and edge views, and in apertural characteristics is very much like the neotype. However, the agglutinant is made up primarily of sponge spicules associated with angular rock fragments and grains. The spicules are more or less aligned in direction of the elongation of the crescentic chambers and are rare or absent on the surface of the first formed chambers. The test dimensions are: Maximum and minimum diameter in spiral/umbilical views, 560 and 480 μm; axial height (thickness) 200 μm. The specimen, ZF 4207, from the same locality, is shown only in its attached position (Figs 23, 24). It is cemented to a bivalve fragment between two ribs and the final very large, broadly crescentic chamber is partly obscured by an overhanging rib and by its own secreted surrounding spongy, calcareous material. The maximum and minimum diameter of the test are 390 and 320 μm, respectively. Again, there are a total of 11 chambers arranged in just over 2 whorls.

Most probably, therefore, this species is able to attach itself to a substrate like *Trochamminella siphonifera* or *Tritaxis australis* sp. nov. described below (p. 299, Figs 15–18), which both have free and attached individuals. Where only attached specimens are available the correct generic assignment (*Tritaxis* or *Trochamminella*) can only be made if the apertural characteristics are known and that means removing at least one specimen from its shell or rock fragment and cleaning up the umbilical side so that the aperture can be seen.

For the present the specimen described and figured by Hedley *et al.* (1964) as *Tritaxis fusca* from shore sand, Isle of Skye, is left in open nomenclature. Its small size, chamber number and appearance both in edge and umbilical view, are atypical of Williamson's species.

Genus: ***TRITAXIS*** Schubert, 1920, emend

EMENDED GENERIC DESCRIPTION. Test free or attached, plano-convex, trochospiral; final whorl typically with 3 spirally crescentic chambers, final chamber making up about half of umbilical side; wall agglutinated, imperforate; aperture a single interiomarginal extra-umbilical opening with borders resting on first chamber of final whorl; attached specimens surrounded and glued to substratum by spongy calcareous substance (no tunnel-like radial extensions observed).

TYPE SPECIES. *Rotalina fusca* Williamson, 1858. Neotype erected herein, Recent, N Atlantic. Distribution possibly worldwide.

REMARKS. The aperture of *Tritaxis* is fundamentally the same as that of *Trochammina* Parker & Jones, 1859 (type species: *Nautilus inflatus* Montagu, 1808). On the basis of the aperture alone, *Tritaxis* could be regarded as a junior synonym of *Trochammina* (see Cushman, 1928: 171). However, in our new classification of the Trochamminacea (Brönnimann *et al.,* 1983) the adult growth form or overall shape of the test can be of generic significance, at the same level in the classificatory framework as the apertural features. The adult growth form of *Tritaxis* is a particular arrangement within the Trochamminidae. By its plano-convex test and umbilically flattened chambers of the final whorl, the test is well adapted to attachment. The only other occurrence where we find this arrangement is in *Trochamminella,* which however differs by its areal aperture from *Tritaxis.* On the basis of apertural features and adult growth form the generic status of *Tritaxis* is retained.

During our examination of the *Terra Nova* Collections in the BM(NH) (Heron-Allen & Earland, 1922), we came across some material from off New Zealand, identified as '*Valvulina fusca* (Williamson)' (loc. cit., p. 125). There are two species involved, one is the true *Tritaxis fusca,* the other is here described as new.

Tritaxis australis sp. nov.
Figs 15–18

DIAGNOSIS. A pointed, high conical *Tritaxis* with very coarse agglutinated wall. 4 chambers on umbilical side, but sutures indistinct both spirally and umbilically. Aperture distinct.

NAME. *Australis*—southern. Referring to its occurrence in the Southern (Pacific) Ocean, off New Zealand.

MATERIAL. 2 specimens from *Terra Nova* station 96 (Heron-Allen & Earland station 6), 7 miles E of North Cape, New Zealand (long. 173°04′E, lat. 34°23′S), depth 70 fathoms (128 m), ex Heron-Allen & Earland type-slide 286 (material 96C), collected 3rd August 1911. Labelled in their faunal-slide collection notes as '*Valvulina fusca* (Williamson)'. Formally designated as holotype (ZF 4204) and paratype (ZF 4205).

HOLOTYPE. ZF 4204, illustrated in oblique-umbilical, edge and umbilical views in Figs 15–17 by Scanning Electron Microscopy.

DESCRIPTION (HOLOTYPE). Test free, sinistral trochospire, plano-convex, pointed and conical. Outline in umbilical and spiral view suboval, in edge view triangular with compressed-rounded periphery but not carinate. Umbilically very shallow-concave, with closed axial depression (umbilicus). Agglutinant coarse and sutures difficult to discern, chamber number therefore not known with certainty. Final whorl with 4 chambers, elongate-crescentic spirally, more or less flattened umbilically. First chamber of final whorl is umbilically a small wedge, followed by larger, almost equidimensional second and third chambers; final chamber occupies about one-third of umbilical side. The single aperture is an interiomarginal, small arch-like opening with a distinct but narrow rim. It rests with its border completely on the surface of the first chamber of the final whorl and is eccentric in respect to the axis of coiling. Agglutinated wall is apparently single-layered and imperforate. Coarse agglutinant consists of rock fragments and derived organic components.

DIMENSIONS (HOLOTYPE). Maximum and minimum spiral/umbilical diameter 510 and 460 μm, respectively; axial height (thickness) 330 μm. Maximum diameter of aperture 45 μm.

VARIATION (PARATYPE). ZF 4205 (Fig. 18) is attached to a bivalve fragment. It is indistinguishable from the spiral side of the holotype. Surrounding the test there is a little secreted spongy material into which are incorporated some foreign elements. There are no tunnel-like projections as normally found in the spongy mass of *Trochamminella siphonifera* Cushman. Maximum and minimum spiral/umbilical diameter, respectively 540 and 480 μm; axial height (thickness) c. 330 μm.

REMARKS. *T. australis* differs by its pointed, high conical test and its coarse agglutinated wall from the spirally, lower, domed plano-convex test (with finer agglutinant) of *T. fusca* (Williamson). In the final whorl of *T. australis* there are 4 chambers, whereas there are typically 3 in *T. fusca.*

II. On *Trochamminella* Cushman

In 1943 Cushman proposed *Trochamminella,* a new Recent trochamminid genus. It was defined as follows:

> Test trochoid, free in the early stages, sometimes attached in the later stages; wall arenaceous, aperture in the unattached forms a rounded opening near the margin of the ventral face of the last formed chamber, usually surrounded by a slightly raised ring; the attached adult surrounded by an irregular rim of material similar to that of the wall and extending out in a tabular neck with rounded aperture.

This definition is based on *Trochamminella siphonifera* Cushman (1943; 95, pl. 16, figs 18–20) which was at the same time designated type species. It is from the Johnson-Smithsonian Expedition station 25, off Puerto Rico, depth 240–300 fathoms (440–550 m), and is represented in the collections of the US National Museum, Washington, by the lectotype (reg. no. 39619), a fixed specimen, and 6 paratypes (reg. nos. 39620 and 39621), all free specimens. The two illustrated paratypes (Cushman, 1943, pl. 16, figs 19, 20) have a single, oval aperture close to the base of the final chamber above the first chamber of the final whorl. As the free and attached specimens are morphologically indistinguishable, Cushman assumed that they were conspecific. One of us (P.B.) has examined the types and concurs. His observations are given below.

The holotype is attached to a thin bivalve fragment (see also re-illustration by Loeblich & Tappan, 1955, pl. 3, fig. 7). It has a low trochospiral, plano-convex test with 3 elongate-crescentic chambers in the final whorl. The initial portion of the test is obtusely pointed and the early coiling difficult to discern; Loeblich & Tappan's illustration shows 4 subglobular chambers. The test is 'glued' to the bivalve fragment by a light coloured spongy calcareous mass. It completely surrounds, but does not cover the test and develops a radial tunnel-like extension with a fairly thick wall and a rounded terminal opening. The true aperture of the holotype is not known but it has to be assumed that it is of the same type as shown by the free paratypes. The wall of the holotype is finely agglutinated, also light coloured and some sponge spicules occur in the agglutinant. The free paratypes have all the single areal opening situated just above the suture with the first chamber of the final whorl. The opening is completely surrounded by an agglutinated rim. Spirally, all the types have 3 elongate-crescentic chambers in the final whorl. The early enrolment, where it is visible, consists of 4 subglobular chambers arranged in a coil around the subglobular proloculus.

Loeblich & Tappan's (1955: 19, pl. 3, figs 5a–c, 6; 1964: figs 177: 2a–c, 3) specimens from the F.C. *Helga* haul SR 331, off SW Ireland (see p. 291, above) and referred by them to *Tritaxis fusca* (Williamson) have the same morphology and areal aperture as Cushman's type specimens of *Trochamminella siphonifera* from Puerto Rico, and hence they clearly represent the latter taxon. Brönnimann's observations on the *Helga* specimens of the so-called *Tritaxis fusca* in the USNM (reg. nos. P 2198a, b) already discussed (p. 292), have clearly shown them to be really *siphonifera.* One unfigured specimen is attached and shows a long curved tunnel-like extension going radially out from the spongy mass by which the individual is attached to the bivalve fragment. Another attached specimen (see Loeblich & Tappan, 1955, pl. 3, fig. 6; 1964, fig. 177: 3) shows a fairly large, flattened and irregularly contoured spongy mass but no tunnel-like extensions.

In view of these facts, *Trochamminella* is clearly distinct from *Tritaxis* as emended above, and should not be suppressed as a junior synonym of the latter as proposed by Loeblich & Tappan, 1955, 1964 and by Hofker, 1976, 1979). *Trochamminella* is now also emended in the light of our re-evaluation of the situation.

Genus: ***TROCHAMMINELLA*** Cushman, 1943 emend

EMENDED GENERIC DESCRIPTION. Test free or attached, plano-convex, trochospiral; final whorl typically with 3 spirally crescentic chambers, final chamber making up about half of umbilical side; wall agglutinated, imperforate; aperture a single areal opening near the suture between the first and last chamber of the final whorl; attached specimens surrounded and glued to substratum by spongy calcareous substance which may develop tunnel-like radial extensions with terminal openings.

TYPE SPECIES. *Trochamminella siphonifera* Cushman, 1943. Recent, Atlantic and Caribbean.

REMARKS. *Trochamminella* is a close isomorph of *Tritaxis* but differs from that genus essentially on apertural features. Both genera have single apertures: interiomarginal, of *Trochammina*-type in *Tritaxis,* and areal in *Trochamminella.* As in the case of *Tritaxis,* also in *Trochamminella,* the adult morphology is here considered to be of generic significance: both have a plano-convex test, highly adapted for fixation to a substratum and typically with 3

chambers in the final whorl, crescentic on the spiral side, flattened on the umbilical, with the final chamber making up more or less half of the umbilical side. To be consistent, now all other trochamminids with different adult morphology, but with the same type of interiomarginal or areal aperture, will have to be placed in different genera. For species with a single areal aperture near and parallel to the base of the final chamber, but possessing a different type of adult morphology to *Trochamminella* (free, biconvex tests with inflated chambers), Frerichs (1969) introduced the Recent genus *Pseudotrochammina,* with *P. triloba* from the deep waters of the Gulf of Mexico as type species (Frerichs, 1969: 1, pl. 1, figs 3a–d; pl. 2, figs 3a, b). Pending a full evaluation of this genus, the Recent *Ammoglobigerinoides* Frerichs (1969) and the Palaeocene *Conotrochammina* Finlay (1940), now in preparation, we tentatively place the following Recent species in *Pseudotrochammina*: *Conotrochammina kennetti* Echols, 1971, Antarctic, Scotia and Weddell Seas, deep water; *Pseudotrochammina mexicana* Frerichs, 1969, Gulf of Mexico, deep water; *Pseudotrochammina triloba* Frerichs, 1969, Gulf of Mexico, deep water; *Trochamminella bullata* Höglund, 1947, Skagerrak, depth 500–700 m; *Trochamminella atlantica* Parker, 1952, North Atlantic, off Portsmouth, New Hampshire, shallow water.

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A lectotype for *Jadammina macrescens* (Brady) and emendation of *Jadammina* Bartenstein & Brand (Protozoa: Foraminiferida)

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Introduction and historical review

H. B. Brady (*in* G. S. Brady *et al.*, 1870: 290), in a study of the foraminifera of tidal rivers of the British Isles, introduced the name *Trochammina inflata* var. *macrescens* for a ... 'nautiloid complanate form' which he regarded as related to *T. inflata* (Montagu), not on morphological grounds but on an affinity shown by the ... 'extreme tenuity of the test, its membranous nature, and its agreement in chemical relations'. This, he believed, to be the consequence of 'depauperating' in particular environments where calcium carbonate was a rare mineral element. Brady (*ibid*: 290, pl. 11, figs 5a–c) described his new variety as follows:

> Test nautiloid, complanate. Chambers numerous, thin, concave. Septal plane narrow. Texture membranous, subarenaceous, scarcely calcareous. Colour brown. Long diameter 1/65 inch [390 μm].

Nothing is said about the apertural features which were obviously taken to be the same as in *T. inflata.* Furthermore, the coiling is erroneously stated to be planispiral. Brady had a wide notion of the species concept and it would be natural that he would consider his variety *macrescens* as conspecific with *T. inflata* as expressed by his title to the description. On the other hand he did recognise differences in coiling and agglutination between the two, and concluded, somewhat ambiguously that 'pending the re-arrangement of the group, it has been thought best to give a sort of varietal distinction to the complanate specimens above mentioned; and a separate line is accorded to them, under the name *T. macrescens,* in the Table.' In this table where Brady lists the geographic distribution of the brackish water species from Britain, the variety *macrescens* is however suddenly accorded specific status and listed as '*Trochammina macrescens* nov. spec.' Subsequently, in his 'Synopsis of the British Recent Foraminifera', Brady (1887: 892) reverted to varietal status for the taxon with the annotation ... 'I have great doubt as to the propriety of retaining this form under a distinct name. The examination of a considerable series of specimens suggests that it represents only the depauperated condition of *Trochammina inflata*:—in other words, that when *Trochammina inflata* lives in pools, the water of which contains a very small proportion of mineral constituents, the test loses its firm shelly consistence and becomes little more than a chitinous envelope, so thin that the inflated contour of the segments is lost when the specimens are taken out of fluid and dried'. The last part of the sentence refers to what we now call 'collapse features'. In material from the Trinidad mangrove swamps, we have in fact seen individuals of a trochamminid which were in this 'depauperated condition' but which did not always show collapse features, and may indeed be referable to the true *T. inflata* (see also remarks by Bartenstein & Brand (1938: 384) on the preservation of *Jadammina polystoma* and *Trochammina inflata*).

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Brady did not select a type specimen of *T. inflata* var. *macrescens* and as his illustrations (1870, pl. 11, figs 5a–c) showed only the general aspect of the test, the low trochospiral enrolment and collapse features in a very poorly agglutinated wall, later workers could not be sure what *macrescens* really was. In order to clarify the situation Brady's remaining syntypic specimens in the British Museum (Natural History) have been studied and a lectotype proposed. It will be shown that Brady's form represents a trochamminid species totally distinct from *T. inflata*. However, before describing the lectotype, a few other historic and taxonomic aspects of the *macrescens* problem have to be considered.

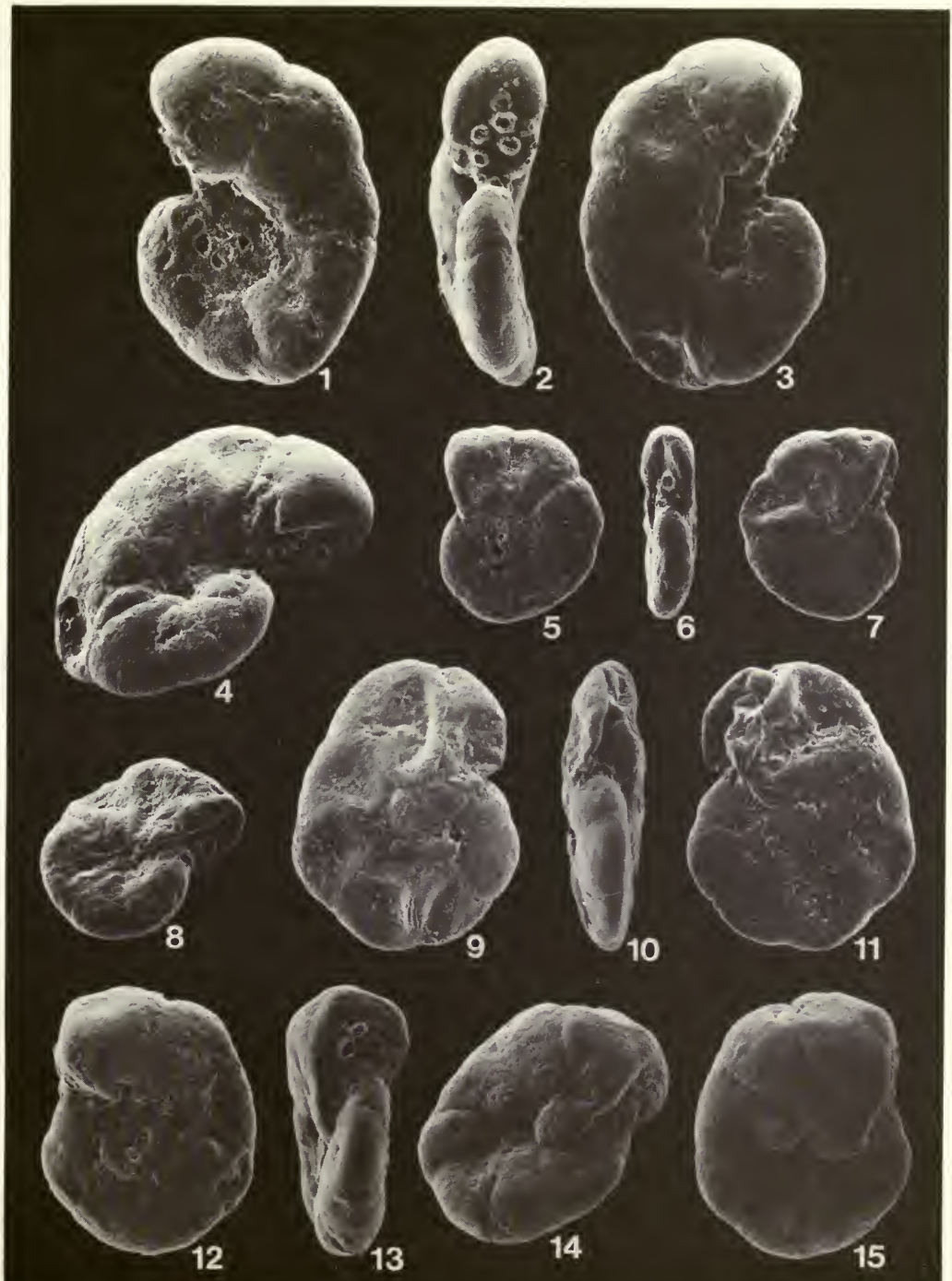
Bartenstein & Brand, and Bartenstein alone, published in 1938 two papers on the foraminifera of the tidal flats of the Jade area at Wilhemshaven, N. Germany. In the first paper they introduced *Jadammina polystoma* gen. et sp. nov., and in the second Bartenstein described the general aspects of the foraminifera of the Jade area. *J. polystoma* Bartenstein & Brand (1938: 382, figs 1–3) was described as follows:

> Gehäuse kegel-spiral, aber niedrig. Spiralseite flach, alle Kammern sichtbar, Anfangskammer und innerste Windung oft vertieft. Nabelseite eingesenkt, nur die Kammern der letzten Windung sichtbar. Bei ausgewachsenen Tieren besteht ein Umgang aus 8–10 Kammern, die breiter als hoch sind. Die Nähte sind schwach vertieft, der Gehäuse-Rand leicht gelappt. Die Nähte sind—vor allem bei älteren Tieren gut zu beobachten—schwach S-förmig geschwungen. Die Mündung besteht aus einem Mündungs-schlitz an der Basis der Endkammer sowie aus Mündungslöchern, die auf der Stirnseite der Endkammer sitzen. An den Mündungslöchern ist die Gehäusewand aufgeworfen, sodass die Mündungslöcher in kurzen, halsartigen Fortsätzen sitzen. Ihre Zahl schwankt swischen 3 und 7 Mündungslochern, der Typus besitzt 5. Die Anordnung der Löcher zueinander ist nicht regelmässig, obwohl häufig die Gestalt eines gleichschenkeligen Dreiecks erscheint (Abb. 2a–1). Schale: Pseudochitin-Tapete, in die kleine Quartzkörner vollkommen eingebacken sind; kalkfrei. Gehäuse häufig mit eingefallenen Wänden (vgl. Teil C). Farbe: braun, selten grau. Durchmesser des Gehäuses: 0·24 mm.

Bartenstein & Brand (1938: 383) presumed that Brady's *T. inflata* var. *macrescens* could also be a *Jadammina* but yet different from their *polystoma* because, they argued, Brady certainly would have seen and described the multiple aperture if it had existed. The illustrations of Brady (1870, pl. 11, figs 5a–c) however show a very low, strongly collapsed trochospire in which the apertural features are not recognisable. Bartenstein & Brand made a search for Brady's figured specimens but apparently without success and Dr K. P. Oakley of the British Museum (Natural History) stated in correspondence at the time, that they were presumed lost. In conclusion, they considered *T. inflata* var. *macrescens* and their *J. polystoma* to be different, but ecologically related, trochamminids.

Bartenstein & Brand's conclusion was accepted by some workers, however often with mixed feelings, while being refuted by others.

Phleger & Walton (1950) elevated Brady's variety to species rank. This was followed by Parker (1952: 408) who remarked that the species mentioned by Phleger & Walton (1950) ... 'should be referred to *Jadammina polystoma* Bartenstein & Brand. The two forms [*T. macrescens* and *J. polystoma*] appear to be distinct and have not been found together at the same locality'. Parker & Athearn (1959) also recognised both taxons but considered it ... 'possible that this species [*J. polystoma*] and *Trochammina macrescens* are related or even identical'; they found in Poponesset Bay, Massachusetts, that the two forms lived together. Adams & Haynes (1965), in their paper on the marsh faunas at Borth, W Wales, seem to have been the first to synonymise the two names under *Jadammina macrescens* (Brady). Bartenstein (1969) reviewed the worldwide geographic distribution of *J. polystoma* and *T. macrescens* but still continued to distinguish the two. The overall trochospiral morphology of both forms being virtually identical, he based the distinction on the apertural features only: a single interiomarginal slit in *T. macrescens* and a multiple aperture consisting of a peripheral interiomarginal slit and a variable number of areal pores, in *J. polystoma*.



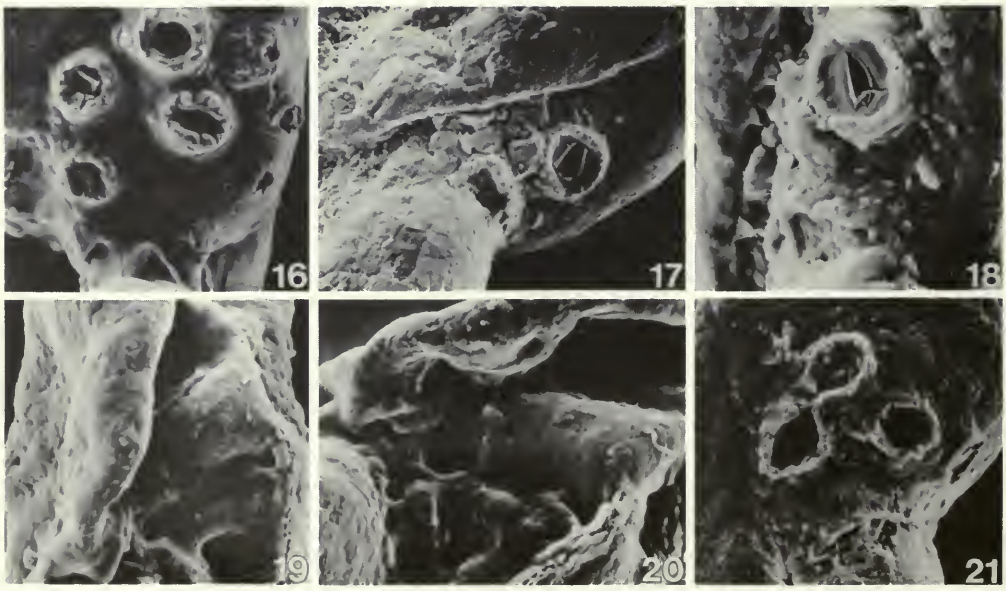
Figs 1–15 *Jadammina macrescens* (Brady). Figs 1–4, Lectotype (ZF 4212). Spiral, edge, umbilical and oblique-umbilical views. Figs 5–8, specimen ZF 4211. Spiral, edge, umbilical and oblique-umbilical views. Figs 9–11, Paralectotype (1955.10.28.2). Spiral, edge, and umbilical views. Figs 12–15, Paralectotype (ZF 4213). Spiral, edge, oblique-umbilical and umbilical views. All ×105. Figs 1–4, from River Blyth, NE England; figs 5–8, from Montrose Basin, E Scotland, at low water; figs 9–11, locality unknown, but probably River Blyth; figs 12–15, from Loch Gruinart, Islay, W Scotland. All from brackish water. Ex Brady collection, BM(NH).

As Brady's original specimens were apparently not available and the 1870 illustration unfortunately does not show the aperture (the final chamber is strongly deformed), Bartenstein's suggestion (1969) that the aperture of *T. macrescens* is a single interiomarginal slit is subjective, interpretative and not factual.

The synonymy proposed by Adams & Haynes (1965) was also accepted by Murray (1965; 1971) and followed again by Haynes (1973: 41, pl. 1, fig. 5; pl. 2, figs 14–16; text figs 7: 1–5) who published the first revision of Brady's species using as comparative material syntypic specimens from Westport (W Ireland), deposited in the British Museum (Natural History). Haynes described *Jadammina macrescens* in detail and remarked that ... 'the apertures are frequently obscured in this delicate species which is prone to collapse on drying or burial in sediment. As, in any case, the development of the areal apertures appears to be a variable feature it becomes merely an academic exercise to attempt to distinguish *Trochammina macrescens* from *Jadammina polystoma.* After examination of the excellent material of Brady from Westport in the British Museum we agree with Parker and Athearn who suggested that these specimens were virtually identical'. Although having seen Brady's collections of *T. inflata* var. *macrescens,* Haynes did not select a lectotype. The problem has therefore remained unsettled to this day giving further occasion to discussions and speculations about whether *macrescens* and *polystoma* are in fact synonyms or not (see Scott, 1976 and Scott & Medioli, 1980).

A lectotype for *Jadammina macrescens* (Brady)

The present writers have examined the complete syntypic series of specimens labelled *T. inflata* var. *macrescens* or '*T. inflata* brackish var', together with other material, in the Brady collection, British Museum (Natural History). The extant syntypes are from the following places listed in Brady's 1870 'Table of Localities': Rivers Wear and Blyth, Northumberland



Figs 16–21 *Jadammina macrescens* (Brady). Apertural detail. Fig. 16, Lectotype (ZF 4212). Edge view showing interiomarginal slit in peripheral position and areal pores, ×350. Figs 17, 18, specimen ZF 4211. Oblique and edge view of interiomarginal slit and single areal pore, ×390 and ×650 respectively. Figs 19, 20, Paralectotype (1955.10.28.2). Edge and oblique views of strongly deformed apertural face, ×400 and ×475, respectively. Fig. 21, Paralectotype (ZF 4213). Edge view showing peripheral interiomarginal slit and areal pores, two of which are interconnected, ×295.

and Durham; Loch Gruinart (or Grunard), Islay, and Loch Gilp, Scotland; and Westport, Ireland. An examination of the illustrations of *T. inflata* var. *macrescens* in Brady, 1870, shows that pl. 11, figs 5a–c, are of two different individuals. The umbilical view is of a 9-chambered, and the spiral view, of an 8-chambered specimen. The apertural (edge) view, fig. 5b, which is connected with the umbilical view (fig. 5a) in Brady's illustration by a dashed line, is therefore probably the same specimen. We tried to find the individuals which served as the originals to Brady's figures and encountered a specimen (reg. no. 1955.10.28.2) marked 'Syntype. Brackish water' (the locality is uncertain, but is probably River Blyth) which corresponds closely to his illustration of the spiral view (fig. 5c). We have re-illustrated it by Scanning Electron Microscopy in our Figs 9–11, 19, 20. Compare in particular the outline on the test, the number of chambers, details at the base of the first chamber of the final whorl, and the collapse features. The final chamber is strongly deformed through collapse. The detailed views of the inturned apertural face (Figs 19, 20) show at least 3, possibly 4, areal pores as are developed in *Jadammina polystoma.* The primary aperture can be seen best in the general edge view, Fig. 10. It is an *interiomarginal peripherally situated narrow slit.* In our opinion, the features of this individual are the same as those of *J. polystoma.* But as the aperture face is strongly deformed and the presence of areal pores may be disputed, it was considered best not to select it as lectotype. The other figured specimen shown in Brady's pl. 11, figs 5a, b, could not be found and apparently does not exist any more in the British Museum (Natural History) Collections.

Instead, a well preserved specimen from Brady's syntypic slide reg. no. 64.4.3.37, from the brackish waters of the River Blyth, Co. Durham, NE England (long. 1°33′W, lat. 55°08′N), has been selected and is here formally designated as lectotype of *Jadammina macrescens* (Brady) (= *Trochammina inflata* var. *macrescens* Brady, 1870). It is illustrated by Scanning Electron Microscopy in our Figs 1–4, 16, and is re-registered under the BM(NH) no. ZF 4212.

Description (lectotype). Test free, very low dextral trochospire; tendency to planispiral coiling in adult test. Outline in umbilical and spiral view elongate-oval, faintly lobate in final portion; in edge view, compressed with rounded peripheries. Umbilical side with well defined umbilical depression, spiral side also depressed in early part through onlap of rather inflated chambers of final whorl on less inflated proceedings chambers. Final whorl of 9 chambers, total number of chambers not determined but probably between 18 and 20. Radial sutures spirally and umbilically well defined, straight to slightly incurved. Aperture multiple: a single interiomarginal slit in peripheral position and 7 or 8 rounded areal openings surrounded by granular rims. Wall agglutinated, organic base dominant, probably single layered and imperforate. Colour of test, dark brown. No collapse features, but spiral wall of early chambers destroyed.

Dimensions (lectotype). Maximum umbilical and spiral diameter of test 490 μm, minimum diameter 290 μm, thickness (axial height) 110 μm. Radial and maximum tangential diameter of final chamber 200 μm, thickness about 145 μm. Height of interiomarginal aperture 10 μm, maximum diameter of areal apertures 30 μm.

Variation (paralectotypes). Two paralectotypes are selected and figured herein. The first, reg. no. 1955.10.28.2 (Figs 9–11, 19, 20), is probably from the River Blyth, like the lectotype. Its morphology has already been discussed above, save for its dimensions which are: maximum and minimum diameter of test, respectively 390 and 300 μm, and thickness (axial height) 110 μm. The second paralectotype (ZF 4213) comes from slide no. 64.4.3.34, Loch Gruinart (Grunard), Isle of Islay, W Scotland (long. 6°20′W, lat. 55°49′N), and has maximum and minimum test diameters of 370 and 300 μm respectively, and a thickness (axial height) of 150 μm. It has an exceptionally well preserved test, especially in the apertural face. It is illustrated in Figs 12–14, 21. It differs from the lectotype in having a tighter coil, more globose early chambers, a more restricted umbilicus (produced by embracing lobe of last formed chamber) and having fewer areal pores.

OTHER SPECIMEN. A further specimen is illustrated (Figs 5–8, 17, 18 (ZF 4211)) from Montrose Basin, E Scotland (long. 2°31′W, lat. 56°43′N). It is from the Brady Collection (ex slide 64.4.3.18), but is not from the syntypic series. It is small, and has only one areal pore. Dimensions are: maximum and minimum diameters in umbilical and spiral views, respectively 260 and 230 μm, thickness (axial height) 80 μm.

REMARKS. The lectotype is virtually identical in its morphological features with Bartenstein and Brand's type specimen of *Jadammina polystoma* (Bartenstein & Brand, 1938, figs 1a–c (on p. 382)), excepting in the number of areal pores which is 5 in the latter against 7 or 8 in the former. As has been shown by Bartenstein & Brand (1938, fig. 2) the number of pores is a feature that varies individually. Indeed, we show a paralectotype (ZF 4213) with 4 areal pores (two separate, and two interconnected) and a further specimen (ZF 4211) with only a single pore. Of primary taxonomic importance in *macrescens* and *polystoma* is the peripheral position of the interiomarginal aperture which gives the superficial appearance of planispiral enrolment. The early enrolment of the lectotype is distinctly trochospiral, it has therefore to be assumed that during early coiling the position of the interiomarginal aperture was in an umbilical rather than peripheral position. This apparent planispiral enrolment in the adult was the reason for Brady's (1870) mistaken interpretation of the coiling as 'nautiloid complanate'.

In conclusion, *T. inflata* var. *macrescens* is a *Jadammina.* Bartenstein & Brand's specific name *polystoma* clearly falls into synonymy with Brady's taxon whose correct name is *Jadammina macrescens.*

Emendation of *Jadammina* Bartenstein & Brand, 1938

Following our morphological description of the type-species, the generic definition is emended herein.

EMENDED GENERIC DEFINITION. Test free, low trochospire, with tendency to planispiral coiling in adult test. Wall agglutinated, imperforate. Aperture multiple, consisting of single interiomarginal slit in peripheral position and one or more areal pore(s) in lower part of septum; pore(s) surrounded by projecting rims.

TYPE SPECIES. *Trochammina inflata* var. *macrescens* Brady, 1870. Recent brackish water. Worldwide in temperate to cool regions unknown in subtropical or tropical mangrove areas.

REMARKS. *Jadammina* differs from *Trochammina* Parker & Jones (type species: *Nautilus inflatus* Montagu, 1808) essentially in apertural features. *Trochammina* has an interiomarginal slit-like umbilical aperture intermediate between the axis of enrolment and the periphery of the test, never in a peripheral position, whereas *Jadammina* has a multiple aperture consisting of a single interiomarginal slit in a peripheral position and supplementary areal pore(s) in the lower part of the septum. *Jadammina* is therefore quite distinct from *Trochammina,* not a junior synonym of the latter as stated by Scott & Medioli as recently as 1980 (p. 44), and a genus in its own right.

Acknowledgements

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A neotype for *Trochammina inflata* (Montagu) (Protozoa: Foraminiferida) with notes on the wall structure

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Introduction

Montagu (1808: 81, pl. 18, fig. 3) introduced under the name *Nautilus inflatus* . . . 'A non-descript species, rarely found amongst sand on the coast of Devon' and characterised it as follows:

> Shell spiral, opaque, brown, with three lobated volutions; in the final whorl are five extremely ventricose articulations, anterior end subglobose: syphon placed as in *Nautilus Beccarii.* It is not so much depressed as that shell, nor are the articulations half so numerous, but vastly more timid; the size inferior.

This description is accompanied by a stylised hand-coloured drawing of the spiral side of a low trochospire with 5 well-separated subglobular chambers of a brown colour, each gradually increasing in size. Montagu's type specimen is lost and his illustration and very general description were of little help for the identification of *N. inflatus* until Williamson revised it in 1858. In his classic work *On the Recent foraminifera of Great Britain,* containing numerous accurate detailed observations, Williamson placed *N. inflatus* in *Rotalina* d'Orbigny and described the species in much more detail. A new and taxonomically important aspect of the revision concerns the apertural features. The position of the aperture is said to be 'septal', placed 'close to the preceding volution' (that is interiomarginal) and 'a little below its peripheral margin'. The umbilical and spiral sides, chamber form and intercameral sutures are all described and the wall texture is given as 'finely arenaceous'. In contrast to Montagu, Williamson called *Rotalina inflata* (Montagu) a 'very distinct species', but still added that it was rare.

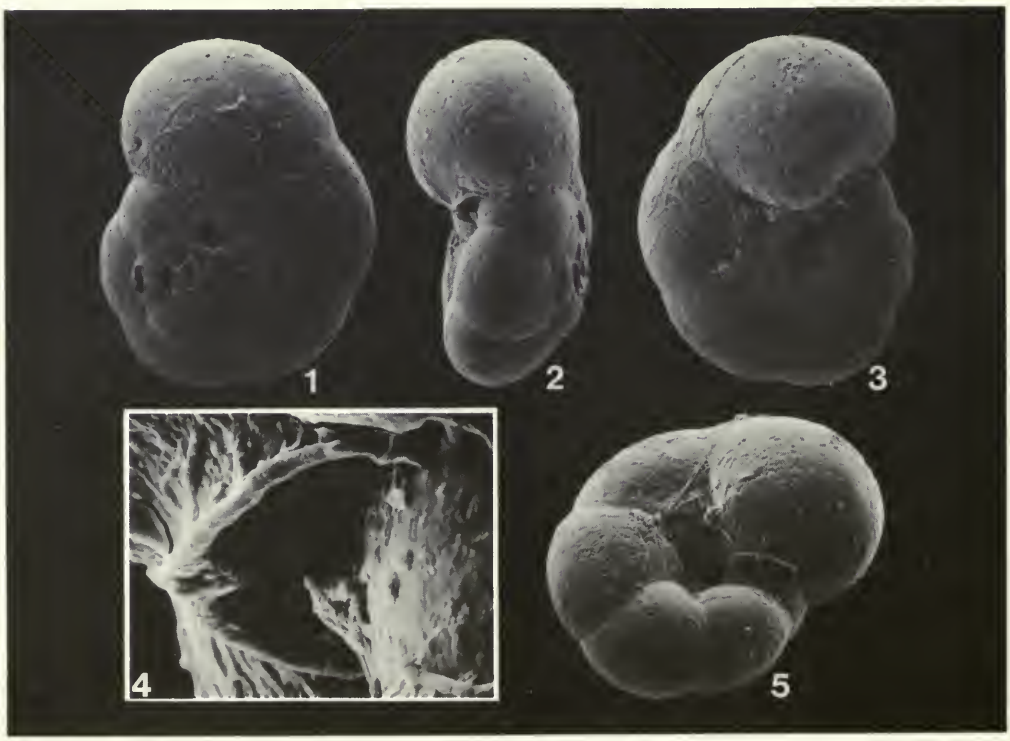
Apart from the coast of Devon, Williamson cited as localities: Weymouth, Swansea, Sandwich (J. G. Jeffrey, collector); Skye, Arran and Shetland (G. Barlee, collector). Williamson's revision (1858: 50, pl. 4, figs 93, 94) not only furnished the first adequate description, but also the first good illustrations of Montagu's species: they show the spiral side of a 6-chambered individual (final whorl) with the characteristic dark brown initial coil followed by two more coils, lighter brown in colour, consisting of subglobular chambers separated by incurved radial sutures (fig. 93); and the umbilical side of a 5-chambered individual with its small, deep axial depression and the straight intercameral sutures (fig. 94). These two specimens are missing from the extant part of the Williamson Collection in the British Museum (Natural History) but his revision proved adequate to define the species so that subsequent workers, at least in European waters, had few difficulties in identifying it.

It was also Williamson's work which provided the basis for Parker & Jones' (1859: 347) taxonomic comments on *N. inflatus* and for their proposition to place it in a few subgenus of *Rotalia* which they named *Trochammina,* a term derived from the Greek *trochos* (wheel) and *ammos* (sand). Their comments are as follows:

This is a *Rotalia* of a typical specific form (as already remarked by Williamson) and characteristic of a subgenus. This sandy-shelled *Rotalia,* exhibiting a structural condition rare, if not unique, among the genus, differs from its congeners so strikingly in this particular, and in its almost globigerine mode of growth, that we propose to refer it to a separate subgenus under the name *Trochammina.*

The etymology of the name *Trochammina* and Parker & Jones' subgeneric definition explain that the essential feature of the new subgenus by which it is distinguished from *Rotalia*, is the sandy nature of the test. This would be, then, one of the first uses of the wall texture for systematic purposes. As to the occurrence of *R.* (*T.*) *inflata*, Parker & Jones find . . . 'its fullest development in shallow water, where it is sometimes very abundant. For instance some of the clay of the Peterborough Fens yields it profusely.' This seems also to be the first remark on the ecology of the species which later was confirmed by Brady (1887: 892) in his 'Synopsis of the British Foraminifera' where he wrote that it is . . . 'Rarely met with except in brackish water'.

Carpenter (1862: 141, pl. 11, fig. 5) not only elevated *Trochammina* to the rank of genus but extended its concept to include as the 'lowest and simplest' form the undivided planispiral tube (*Trochammina* [=*Ammodiscus*] *incerta*), the irregularly enrolled tube (*Trochammina* [=*Glomospira*] *gordialis,* and as the 'highest' form, the multilocular test (*Trochammina inflata*) developed by the segmentation of the undivided tube. With this extreme emendation *Trochammina* lost the particular meaning given it by Parker & Jones who had originally introduced the subgenus for *Nautilus inflatus* only. Furthermore, Carpenter's drawing (pl. 11, fig. 5) does not correspond at all with Williamson's form and is probably not *inflata.* It was much later, in the *Challenger* Report (Brady, 1884: 336), that



Figs 1–5 *Trochammina inflata* (Montagu). Neotype, ZF 4267. Ex E. Milton Collection, slide 1966.1.6.24. From brackish water, near Broadsands, Torbay, Devon. Spiral, edge and umbilical views; detail of aperture (in edge view), and oblique-umbilical view. Figs 1–3, 5, ×100; fig. 4, ×700.

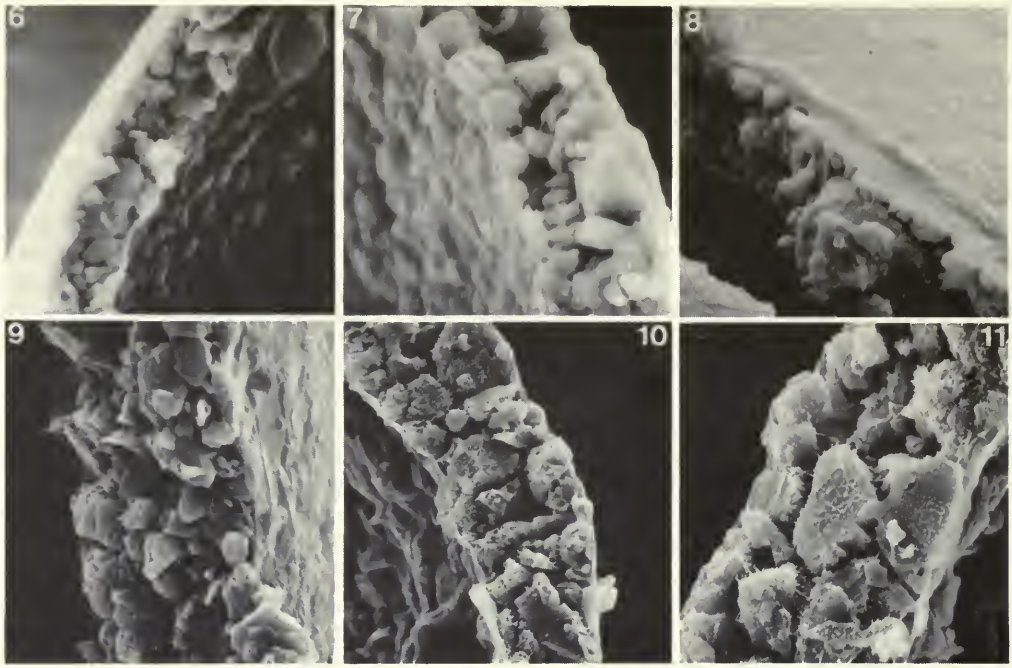
Trochammina was again restricted, this time to include all agglutinated, rotaliform or nautiloid or irregularly coiled, chambered forms. Brady (1884, pl. 41, figs 4a–c) illustrated in three conventional views a typical *T. inflata,* which closely corresponds with the 5-chambered specimen of Williamson's pl. 4, fig. 94. Also Brady's description follows closely that of Williamson. The aperture is characterised as being small and arched, on the inferior side of the final chamber, close to the previous volution, a little within the periphery. The species, according to Brady, is found 'all round the British Islands. It frequents comparatively shallow water, and finds its way into estuaries and other brackish areas.' From this it appears that he thought it was a marine species which was able to survive in lower salinities. Today, we know that it is *restricted* to brackish waters in estuaries, salt marshes, lagoons and mangrove swamps worldwide, and from this environment it may be washed into adjacent marine sediments (Murray, 1971). Although no type of *T. inflatus* exists and Williamson's figured specimens are lost, the species is well defined taxonomically by the revisional work of Williamson (1858) and Brady (1884) and has for the most part been correctly identified in subsequent literature on European waters. Elsewhere, some references to *T. inflata* (e.g. Earland, 1934; Ingle *et al.,* 1980—from marine environments) are known to be incorrect. Nevertheless, it might still be argued that the establishment of a neotype was unnecessary, were it not for the fact that trochamminid classification is now actively under revision (see Brönnimann *et al.,* 1983), and *T. inflata* is particularly important as the type species of *Trochammina* Parker & Jones, which in turn, is type-genus of the subfamily Trochammininae Schwager. It was therefore decided to select a neotype from an assemblage of well preserved individuals in slide 1966.1.6.24 from the E. Milton Collection in the British Museum (Natural History). This material was collected in 1930 from a brackish pool at Broadsands, Torbay, Devon, SW England, and comes from the same county as Montagu's original specimen. The neotype of *T. inflata* has been re-registered as ZF 4267 and is illustrated by scanning electron microscopy in Figs 1–5. The opportunity is also taken to show the aperture and wall structure in detail, the latter, should this potentially important taxonomic criterion be used in future classification of the group (Figs 6–11).

The neotype of *Trochammina inflata* (Montagu)

Description. Test free, a sinistral trochospire; low-convex spirally, shallow-concave umbilically with a small but deep axial cavity. In spiral/umbilical view, outline of test broad-oval, slightly lobate; in edge view moderately compressed, with rounded peripheries. Chambers subglobular, 21 in number (including the proloculus), arranged in $3\frac{1}{2}$ whirls with 6 chambers in final whorl; increasing first slowly, then more rapidly in size. On umbilical side chambers of final whorl triangular and separated by roughly depressed, straight sutures; on spiral side, radial sutures incurved initially becoming straight in final part. Aperture single, interiomarginal, extraumbilical, an elongate open arch resting with its border on the first chamber of final whorl; this low arch extends from edge of axial depression to a subperipheral position, and has a border drawn out from the septal face in form of a collar limited by a thin upturned rim of smooth appearance. Each new chamber covers preceding aperture which therefore does not communicate with axial (umbilical) depression. Wall agglutinated with a finely granular surface texture, slightly more coarse on the umbilical than on spiral side; imperforate. Colour of test brownish, darker initially than in the later chambers.

Dimensions. Maximum umbilical/spiral diameter 470 μm, axial height (thickness) about 250 μm, width of axial cavity 50 μm. Maximum diameter of proloculus 25 μm. Radial and tangential diameters of final chamber 200 and 290 μm, respectively; axial height (thickness) 235 μm. Length and height (centre) of aperture 100 and 25 μm, respectively; width of apertural collar 15–20 μm.

Remarks. The neotype was probably dead at the time of collection and does not show the glossy lustre typical of the surface of living specimens of *T. inflata.* As shown in the SEM



Figs 6–11 *Trochammina inflata* (Montagu). Figs 6–8, ZF 4268, wall broken to show structure: an inner organic layer, a thick agglutinated layer of irregular fragments, and an outer organic veneer. Figs 9–11, ZF 4269. Fig. 9, broken wall showing outer veneer and agglutinated layer; fig. 10, broken wall showing all three 'layers'; fig. 11, broken wall showing in particular nature of agglutinant and cement. ZF 4268 from Broadsands, Torbay, Devon; ZF 4269 from West Williamson, Dyfed. Magnifications between 1500 and 2500.

photographs in Figs 6–11, fresher specimens from the neotype locality and from West Williamson, Dyfed, SW Wales, have an imperforate wall of apparently 3 'layers'. A thin organic inner lining (='tectin lining' of Haynes, 1981, pl. 7, fig. 8), a thick agglutinated layer of medium sized, poorly sorted foreign elements and a thin organic outer layer which covers the middle layer like a veneer. It seems probable that the test of the neotype remained after death for some time in the water and was abraded, thus losing the organic outer layer. The thin algal filaments or fungal threads which criss-cross the surface, particularly on the umbilical side are often seen in death assemblages.

Cushman & Brönnimann (1948: 41, pl. 7, figs 21, 22) described from the mangrove swamps of the west coast of Trinidad, West Indies, a new species which they named *Trochammina laevigata.* It has 5 to 6 chambers in the final whorl (the holotype, pl. 7, fig. 21, has 6 chambers) and by its overall morphology and apertural characteristics appears to be identical to *T. inflata* (Montagu). Although the holotype of *T. laevigata* is much larger than our neotype of *T. inflata,* there is no reason to separate the two. *T. laevigata* Cushman & Brönnimann was also illustrated by Todd & Brönnimann (1957, pl. 4, figs 17, 18) in their paper on the foraminifera from the tidal zone of the eastern Gulf of Paria, Trinidad. The specimen on pl. 4, fig. 17 differs from *T. inflata* by a more lobulate outline and a somewhat higher trochospire, however these differences fall within the variation we have seen in large populations of *T. inflata* from many parts of the world. The other specimen illustrated by Todd & Brönnimann (1957, pl. 4, fig. 18) and referred to *T. laevigata,* is characterised by a *Siphotrochammina*-aperture, and is not conspecific.

Acknowledgements

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The *Conchoecia reticulata* species-group, with descriptions of *C. reticulata* Müller (1906), *C. caudata* (1891), and two new species

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Introduction

G. W. Müller (1906) described *Conchoecia reticulata* from Tiefsee-Expedition material. He states that the shell has a striking sculpture mainly of squares or rectangles which are organised into near-horizontal rows in the dorsal half and descending rows in the ventral half, and that some animals have spines like those of *C. caudata.* This description seems to indicate that there were two forms of *C. reticulata,* a spined and an unspined form.

Since this description several authors have reported *C. reticulata,* Granata & di Caporiacco (1949), Deevey (1968, 1980), Poulsen (1969, 1973), Angel & Fasham (1975) and Angel (1979). The material identified by Granata & di Caporiacco (1949) was undoubtedly the spined form as they used the distinctive carapace spines as one of the characters for their new genus *Macroconchoecia* in which they placed *caudata* and *reticulata.* Deevey (1968) did not mention the spines nor draw them, but in 1980 she confirmed that her specimens, including the specimens described in 1968, bore the distinctive *C. caudata* pattern of spines. Similarly Poulsen (1969) did not make clear whether the six adults caught in the Gulf of Guinea bore spines but later in his 1973 Dana Report he writes that the species is 'easy to recognise by the strong, partly spinous reticulation of the shell' thus implying that all his specimens, including those described in 1969, were spined.

In a recent paper Angel (1979) was the first author since Müller to record two forms of *C. reticulata.* In *Discovery* material from 30°N 23°W he found a smaller deep mesopelagic form characterised by rows of short spines, a larger deeper-living form without spines, and suggested that *C. reticulata* was probably a mixture of two species.

Further examination of *Discovery* material comprising 242 adult specimens led to the conclusion that there were not two forms of *C. reticulata* but three. Besides the spined form and the larger unspined form noted by Angel (1979) there was a smaller unspined form. In the absence of a type specimen or syntypes, I was unable to obtain Müller's Tiefsee-Expedition material, the name *C. reticulata* has been given to the smaller of the two unspined forms. The spined form was excluded on the grounds that it is not the species Müller figured and the terms of his description, whilst clearly including this species, implies that he regarded it as the more atypical form. The larger unspined form was also excluded as the size Müller gave for the male, 3·1 mm is outside the range of 3·4–4·0 mm for the male of this species. Furthermore the depth ranges of the adult spined form and the smaller unspined form are similar, whilst the larger unspined form lives deeper. In *Discovery* samples, with the exception of haul 38 at station 6665 which fished a wide horizon from 1800–3600 m, the adults of the large unspined form and the spined form were not taken in the same haul. Hence it would seem more likely that Müller's unspined form would have been the small species. The large unspined form and the spined form are therefore described below with the names *C. macroreticulata* and *C. spinireticulata* respectively, re-descriptions of *C. reticulata* and *C. caudata* are also provided. Four tables giving precise station data for all material of *C. reticulata, C. macroreticulata, C. spinireticulata* and *C. caudata* identified from *Discovery* collections are stored in the libraries of the BM(NH) and Institute of Oceanographic Sciences.

Bull. Br. Mus. nat. Hist. (Zool.) **46**(4): 317–343 Issued 31 May 1984

Conchoecia reticulata Müller 1906

Conchoecia reticulata G. W. Müller 1906 (*pro parte*) Ergeb. Tiefsee-Exp. **8** p. 64, pl. 12 f 10–17.
Conchoecia reticulata G. W. Müller 1912 (*pro parte*) Das Tierrich—Ostracoda Berlin p. 71.

Male

A male of carapace length 3·1 mm mounted on slides in Euparal and stained with lignin pink has been deposited at the BM(NH) No. 1982: 184. It was caught at *Discovery* station 6665 (10°16·4′N, 19°47·4′W) haul 32 with the N113 (Foxton, 1969).

Carapace (Figs 1A–D). The length of the seven males ranged between 2·8 mm and 3·1 mm averaging 2·99 mm. Only one of the males was sufficiently intact to measure breadth and height of the carapace accurately, both were about 40% of the length. The posterior dorsal corner is nearly a right angle with the left valve corner rounded off and the right produced into a short spine often with a short secondary spine. The left asymmetrical gland opens anterior to the hinge on a small protuberance. Just ventral to the corner, on both valves, are a pair of glands whose function is unknown. The posterior margin is rounded and slanted slightly forwards, along it are scattered edge glands. The posterior ventral corner is strongly rounded and the right asymmetrical gland opens dorsally to it. The ventral edge is nearly parallel to the dorsal edge. In the anterior third it is slightly reflexed outwards and is armoured with small spines derived from extensions of the sculpture. These spines occur on both valves but are larger and more prominent on the left valve. In ventral view the carapace is narrow and smoothly rounded. The rostrum is pointed and short, the length being about one-third the width across the rostral incisure.

The sculpture is distinct, in the dorsal half the markings are largely rectangles which are organised into horizontal rows running parallel to the dorsal hinge. In the ventral half they are more squarrous and run diagonally slanting postero-ventrally. Near the ventral margin the markings become more polygonal, at the centre of each valve and along the posterior margin the markings are weaker and more irregular.

Frontal organ (Fig. 1F). The shaft reaches level with the end of the second segment of the first antenna and the capitulum is downturned, slightly expanded distally. The tip is rounded. Proximally there are long fine bristles on the capitulum, these are concentrated mainly on the vental side and extend half way along its length.

First antenna (Figs 1F & G). The first two segments are subequal and have some discrete patches of short bristles. The *a* seta is shorter than the second segment and has a kink proximally. The *c* seta is a similar length but straight. The *b, d* and *e* setae are all about three times the length of the *a* and *c* setae. The *e* seta carries two rows, each of approximately 50 fine spines which are strongly basally directed. Deevey & Brooks (1980) described them as a 'very thick double row of countless slim lamellae'. The *b* seta has a long, thin, crenulated and horizontally-banded, wing-like callus and a pad with close-set annuli edged with short lateral bristles opposite the distal end of the *e* seta armature. The *d* seta has a few tiny spinules in an equivalent region.

Second antenna (Figs 1E, H & I). The protopodite is nearly 45% of the carapace length, longer than the longest swimming seta which is only 36%. On the endopodite, the *g* seta is three-quarters the length of the *f* seta which is about 43% of the carapace length. The *h, i* and *j* setae are much shorter, about 19% of the carapace length. With the exceptions of the *f* seta, which has a few short bristles distally and the *b* seta which has a few fairly long bristles, the setae are bare. The *c, d* and *e* setae are present.

The hook appendage on the right endopodite has a short straight basal part, with a well-marked process on the anterior side, followed by a sharp bend and a long, curving arm. The tip of the hook is faintly ridged dorsally and armed with a short projection. The left hook appendage is smaller. It lacks a process on the short stalk and has a marked right-angled bend. The main part of the arm is straight. The tip is not obviously ridged but armed with a short projection.

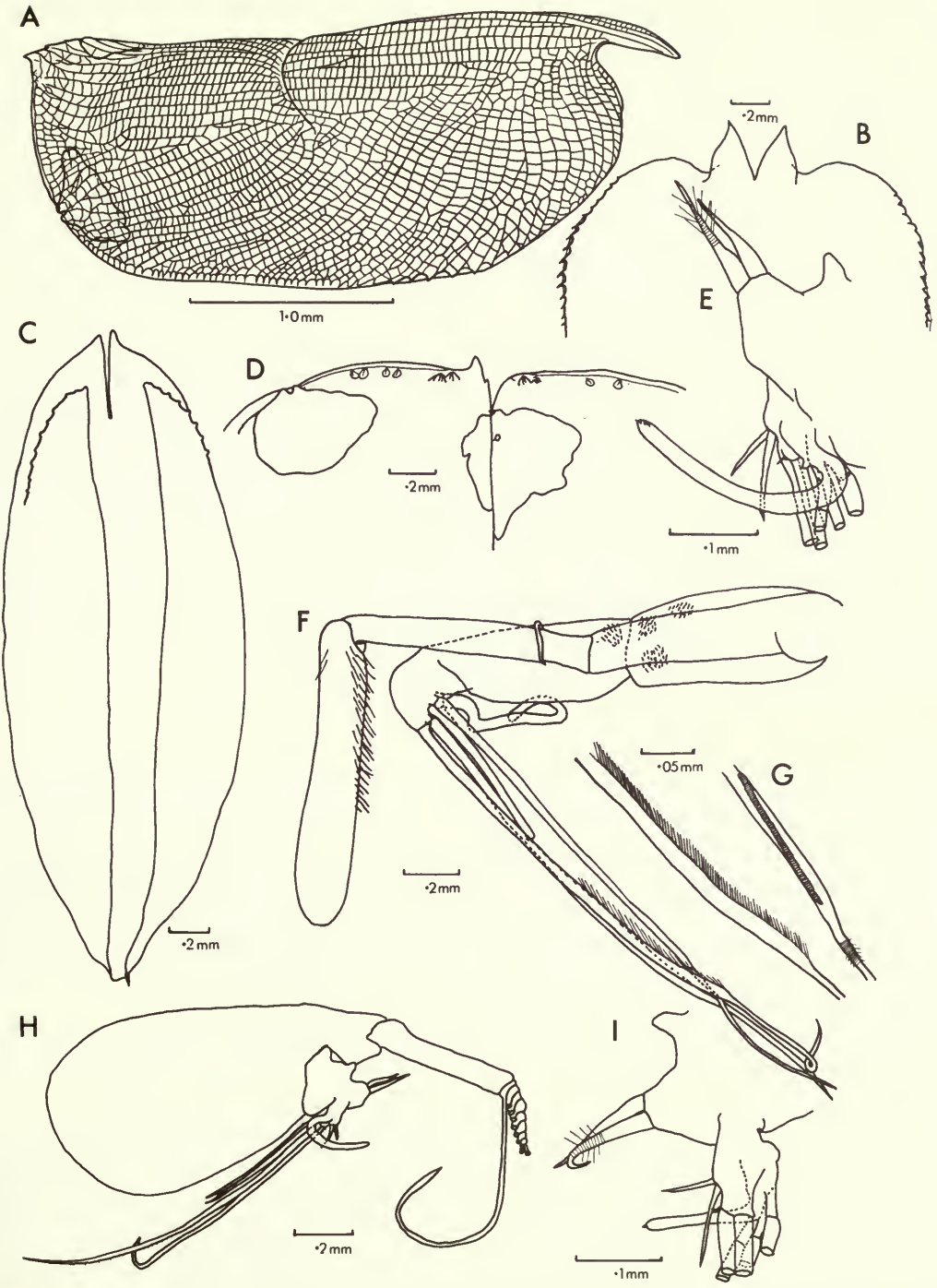

Fig. 1 *C. reticulata* ♂. A: Carapace, lateral view. B: Anterior carapace flattened to show the ventral edge spines. C: Ventral view of carapace. D: Detail of the posterior carapace glands. E: Detail of the endopodite of the right second antenna. F: Frontal organ and first antenna. G: Detail of *b* and *e* setae armatures. H: Second antenna. I: Detail of endopodite of the left second antenna.

Mandible (Figs 2B & E). The basale carries a small seta near the insertion of the endopodite with two long and two shorter setae on the inner face near the toothed edge, the *pars incisa.* The pattern of toothing is typical of the genus, there are several clusters of hairs and a row of hairs below the two spine teeth.

The first segment of the endopodite bears on the outer edge a single seta, with a row of long fine bristles on one side, and on the inner edge four setae, three of which are plumose proximally. The second segment has a fringe of long hairs on the outer edge and bears five setae. The third segment has a large patch of hairs on its inner surface and bears seven setae. The longest terminal claw seta is as long as the total length of the endopodite.

The toothed edge of the coxale has nine teeth. The middle ridge has two tusk-like posterior teeth the inner of which has an irregularly serrate margin followed by 13–14 small teeth. The proximal ridge has 12 irregularly sized teeth, the first, third and fifth posterior teeth being larger than either the teeth between or the anterior teeth.

Maxillula (Figs 2C & H). There is a basal seta. The first endopodite segment has six anterior, one lateral and three posterior setae.

Fifth limb (Fig. 2A). The first segment of the exopodite has several groups of setae. There is a group of four setae near its base, of which two are short and of the two longer setae one is plumose. Above these are two setae inserted laterally, distally there are four more ventral setae and a further two setae more dorsally, one of which is plumose and on a protuberance. The second segment bears two setae ventrally and one dorsally. On the terminal segment the central claw seta is large, robust and bears short bristles distally. The dorsal seta is slightly thicker and longer than the ventral one, both are bare.

Sixth limb (Fig. 2J). The basal segment carries six plumose setae and one bare seta. The second segment has one, bare ventral seta. The third segment has two setae one dorsally and one ventrally placed. The ventral of the terminal bristles is bare.

Caudal furca (Fig. 2G). Each furcal plate carries the eight claw setae normal for adults of the genus and there is a single unpaired seta dorsally.

Penis (Fig. 2F). This is long parallel-sided and blunt-ended with five oblique muscle bands.

Female

A female of carapace length 3·4 mm, stained with lignin pink and mounted on slides in Euparal, has been deposited at the BM(NH) No. 1982: 183. It was caught at *Discovery* station 6665 (10°17·3′N 19°49·0′W) haul 28 with the N113.

Carapace (Figs 3A, C & E). The twelve female specimens and five detached carapaces of females, had a carapace length range of 3·2 mm to 3·4 mm averaging 3·30 mm, a little larger than the males. Overall the shape of the female carapace is similar to the male, but the rostrum is relatively longer, the length is about two-thirds of the width across the rostral incisure. The nature and position of the carapace glands, the pattern of sculpture and the ventral edge spines are the same as the male.

Frontal organ (Fig. 3D). The shaft extends beyond the end of the second segment of the first antenna. The shape of the capitulum is the same as the male. The proximal bristles are short, fine and numerous.

First antenna (Fig. 3D). The limb is well-differentiated into segments, both with discrete patches of short bristles. The dorsal seta is relatively long. The *a–d* setae are about 1/3 of the length of the *e* seta, which is about 1/3 of the carapace length. On the anterior surface of the *e* seta there is, proximally, a row of long fine hairs and distal to these, a row of short bristles which lie nearly flat against the surface of the principal seta. On the posterior surface, opposite the anterior short bristles, there are some slightly longer bristles which are fairly closely spaced proximally, but become more widely spaced distally where the principal seta is broadened and flattened.

Second antenna (Figs 3B & G). The protopodite is about 41% of the carapace length, nearly $2\frac{1}{2}$ times the length of the first exopodite segment. The longest swimming seta is 3/4 the length of the protopodite. On the endopodite the *a* and *b* setae are bare, *c, d* and *e* setae are absent,

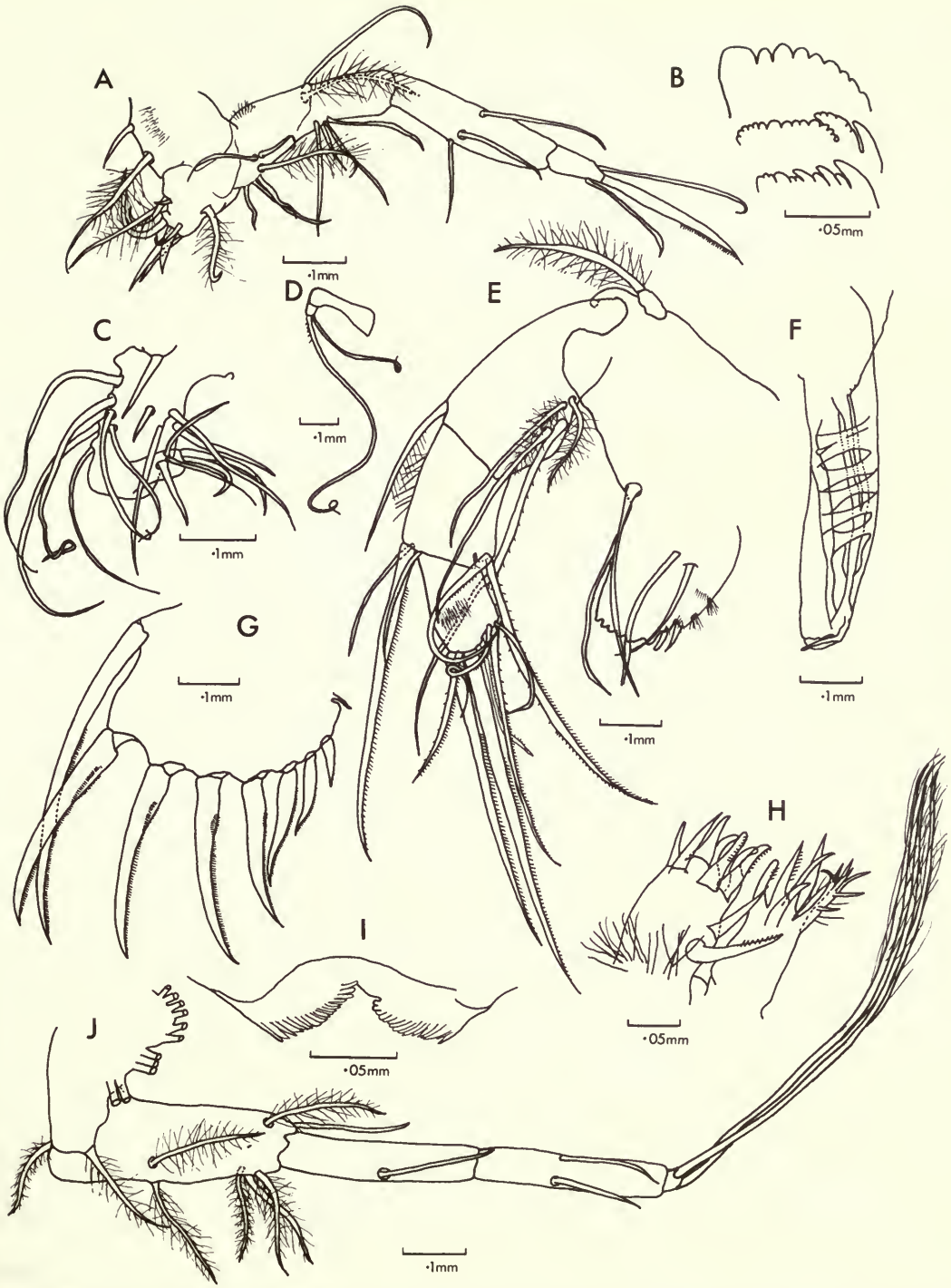

Fig. 2 *C. reticulata* ♂. A: Fifth limb. B: Toothed edge of the coxale and tooth lists. C: Maxillula endopodite. D: Seventh limb. E: Basale, and endopodite of the mandible. F: Penis. H: Coxa of maxillula. I: Toothed edge of labrum. J: Sixth limb.

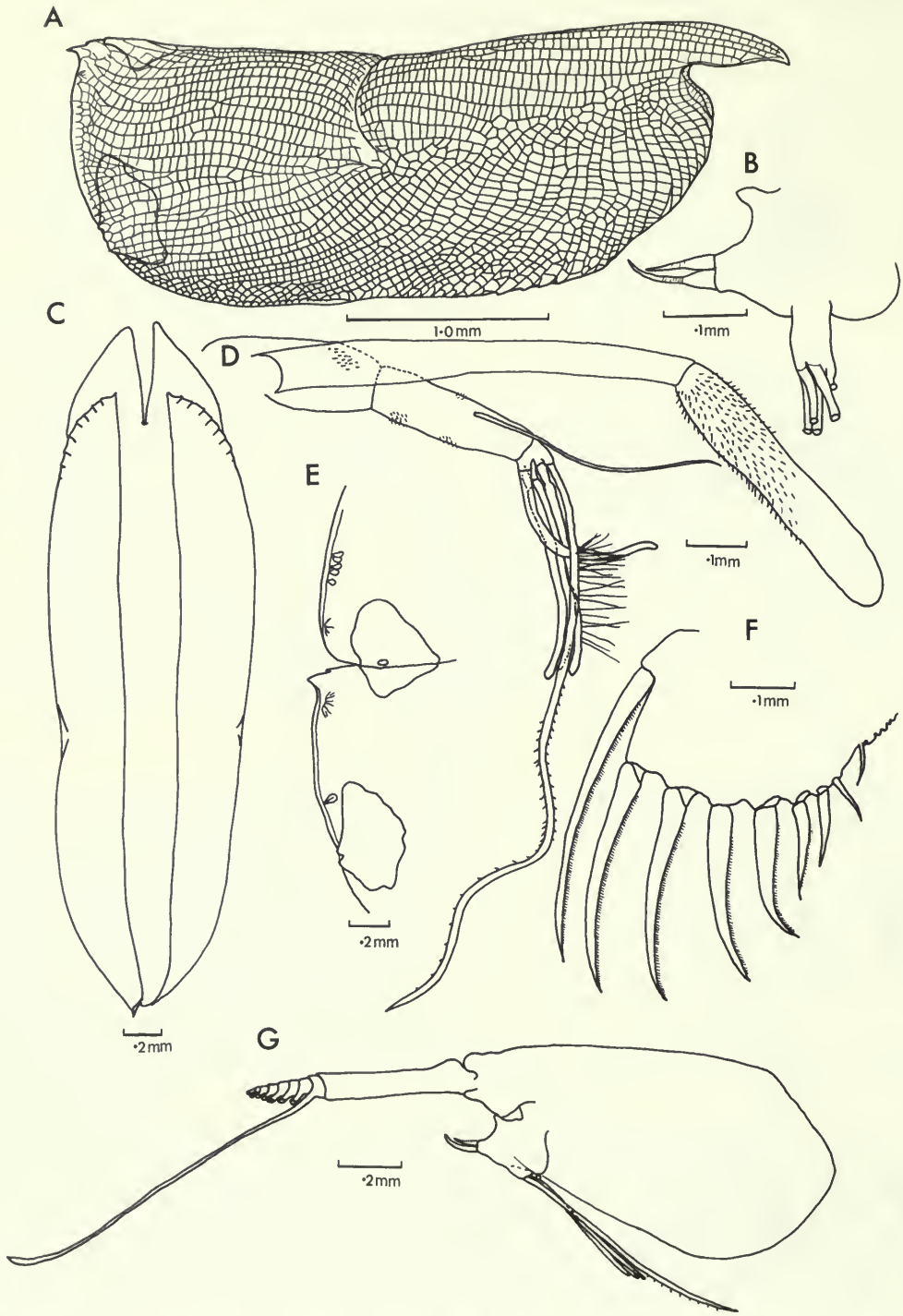

Fig. 3 *C. reticulata* ♀. A: Carapace, lateral view. B: Detail of the endopodite of the second antenna. C: Ventral view of carapace. D: Frontal organ and first antenna. E: Detail of posterior carapace glands. F: Caudal furca. G: Second antenna.

the *f* seta was damaged in all twelve females, the *g* seta is about 24% of the carapace length and carries a few widely-spaced bristles.
Other appendages (Figs 3F & 4A–G). These are all similar to those of the male with the exceptions of the single, outer-face seta of the first segment of the mandibular endopodite which has a row of short bristles rather than the long ones seen in the male, and the usual differences in the sixth limb which are typical of the genus.
REMARKS. 32 specimens were identified from *Discovery* material; all from the comparatively rarely sampled deep meso- or bathy-pelagic levels, at stations between 0° and 20°N in the Atlantic. Besides the seven males and seventeen females there were two stage VI juveniles (2·3 and 2·5 mm) and six stage V juveniles (1·7, 1·8, 1·8, 1·8, 1·8 and 1·9 mm). They were distinguished from *C. macroreticulata* juveniles by the presence of ventral edge spines as well as size and shape. Juveniles seem to occur between 1000–1500 m deep and adults between 1500 m and 2500 m. These depth ranges and the geographic range cannot be regarded as definitive.

Conchoecia macroreticulata sp. nov.

Conchoecia reticulata Müller 1906. M. V. Angel, 1980, *Prog. Oceanog.* **8**, p. 57–58.
Conchoecia reticulata Müller 1906. M. V. Angel, 1981 in *Atlas del Zooplancton del Atlantico sudoccidental* ed. D. Boltovskoy, p. 559 f. 194–77.

Male

The holotype, stained with lignin pink and mounted on slides in Euparal, has been deposited in the BM(NH) No. 1982: 187. It has a carapace length of 3·9 mm and was caught at *Discovery* station 9541 (20°11·4′N 21°40·9′W) haul 26 with the RMT 1 (Baker *et al.*, 1973).
Carapace (Figs 5A, C & H). The length range of the ten males and eleven detached carapaces of males was 3·4 mm to 4·0 mm averaging 3·73 mm. Both breadth and height of the carapace were about 40% of the carapace length. The shape of carapace is fairly similar to that of *C. reticulata* but the ventral edge lacks any projecting spines and the height of the carapace narrows anteriorly. The asymmetrical glands, paired glands and the edge glands are similar in their positions to those of *C. reticulata.* In ventral view the carapace is smoothly rounded, the rostrum is short and pointed. The organisation of the sculpture is similar to that of *C. reticulata* but slightly more pronounced, and the parallel rows in the posterior dorsal quarter rise towards the dorsal hinge.
Frontal organ (Fig. 5E). The details of shape, hirsuteness and relative size of the frontal organ are like those of *C. reticulata.*
First antenna (Fig. 5E). This appendage is similar to that of *C. reticulata* but the proportions of the setae differ. The *c* seta is about three-quarters the length of the *a* seta (Table 1). The *b* and *d* setae are 42%, and the *e* seta 49% of the carapace length, about four times the length of the *c* seta, relatively longer than these setae in *C. reticulata* which are only three times the *c* seta length. The armature of the setae is similar and the *e* seta bears about 50 pairs of spines.
Second antenna (Figs 5B, D & G). The main differences from *C. reticulata* are that the longest swimming seta is relatively longer, as are the *f* and *g* setae.
Sixth limb (Fig. 6H). Some of the plumose setae of the basal segment have rather sparse hairs otherwise this limb is like that of *C. reticulata.*
Penis (Fig. 6E). There are six oblique muscle bands compared to five in *C. reticulata.*
Other appendages. These are all similar to those of *C. reticulata.*

Female

The paratype specimen, carapace length 4·3 mm, stained with lignin pink and mounted on slides in Euparal has been deposited at the BM(NH) No. 1982: 188. It was caught at *Discovery* station 9541 (20°11·4′N 21°40·9′W) haul 26 with the RMT 1.

Table 1 Some morphometric characters of the *reticulata* group of species. Proportions of carapace, frontal organs and first and second antennae expressed as percentages of the total carapace length

	C. reticulata						*C. spinireticulata*						*C. macroreticulata*						*C. caudata**					
	♂	SD	No	♀	SD	No	♂	SD	No	♀	SD	No	♂	SD	No	♀	SD	No	♂	SD	No	♀	SD	No
Range (mm)	2·8–3·1			3·2–3·4			2·8–3·4			3·2–3·9			3·4–4·0			3·8–4·4			4·8–6·1			6·7–7·6		
Mean length	3·0	0·1	7	3·3	0·1	12	3·2	0·2	88	3·7	0·1	80	3·7	0·1	10	4·1	0·2	34	5·6	0·5	5	7·2	0·3	7
Height	40·5	—	1	36·9	—	1	39·1	3·2	19	34·4	1·6	20	40·4	2·4	3	37·5	1·6	14	40·9	2·1	3	41·3	3·1	7
Breadth	39·2	—	1	31·0	—	1	37·9	1·7	12	32·8	2·1	16	39·2	0·6	2	35·9	2·8	10	43·8	3·4	3	43·2	3·9	3
FO capit	17·3	0·6	6	16·5	0·8	12	16·2	0·8	20	16·9	0·8	20	17·2	1·1	9	15·1	0·4	17	22·9	1·2	5	28·9	1·7	8
shaft	26·9	1·1	6	21·9	1·0	12	29·5	1·3	20	21·0	0·8	20	28·0	1·4	9	21·1	0·8	18	32·9	1·6	5	24·7	2·7	8
Ant 1 segt 1	14·6	1·1	6	8·9	1·2	12	17·7	1·2	20	9·6	1·1	18	15·8	1·0	9	9·2	0·7	18	18·3	1·4	5	9·0	1·6	8
„ 2	14·7	1·1	6	8·7	0·5	12	16·0	1·1	20	8·5	0·8	20	15·0	0·9	9	8·9	2·9	18	18·5	0·3	5	10·3	0·5	8
a seta	11·7	0·9	5	10·7	0·5	12	11·3	1·6	18	9·3	0·5	20	12·4	1·5	8	10·8	1·0	18	11·8	1·3	5	12·2	0·6	8
b „	33·6	0·7	5	—	—	—	41·3	1·2	20	—	—	—	41·3	2·7	8	—	—	—	45·1	3·3	5	—	—	—
c „	10·8	0·4	6	—	—	—	8·2	0·9	20	—	—	—	9·2	0·8	9	—	—	—	10·3	0·9	5	—	—	—
d „	33·8	1·7	5	—	—	—	42·1	1·2	20	—	—	—	42·9	3·5	8	—	—	—	48·6	0·9	4	—	—	—
e „	36·3	2·9	—	31·4	1·8	7	48·1	1·3	19	29·0	0·8	16	48·7	3·9	7	32·4	0·8	8	53·3	1·3	4	39·9	1·8	6
Spines	50×2						83×2						50×2						95×2 (+4)					
Ant 2 Protop	44·4	1·4	—	40·9	1·3	12	45·0	1·6	20	39·5	1·1	20	45·6	2·0	5	39·6	1·1	19	49·4	2·9	5	45·6	1·8	8
Exop 1	18·1	1·4	6	17·4	0·9	12	18·1	0·7	20	16·2	0·5	20	18·9	0·6	7	17·5	0·5	19	19·2	0·8	5	18·2	0·7	8
„ 2–8	8·5	1·1	6	6·9	0·3	12	7·8	0·3	20	6·7	0·4	20	7·2	0·3	7	6·7	0·4	18	8·1	0·4	5	8·0	0·6	8
LSS	36·5	4·7	2	34·7	2·8	5	41·4	2·9	19	34·1	2·2	20	44·0	1·4	5	36·8	1·0	11	47·0	2·0	5	41·5	2·0	7
f seta	42·6	2·1	4	—	—	—	51·1	1·8	16	40·2	1·7	11	51·0	3·3	4	—	—	—	60·5	6·7	3	52·7	2·0	4
g seta	33·3	1·8	3	24·2	1·5	4	37·0	1·9	18	25·3	1·0	18	37·6	1·7	5	23·6	2·9	5	40·6	2·4	5	37·3	1·9	7
h i j seta	18·9	1·1	5	18·1	1·1	7	16·1	0·9	20	16·7	1·0	19	17·8	0·8	8	16·1	1·2	10	17·6	1·0	5	21·1	1·6	7

*% values based on carapace length measured from the base of the posterior dorsal spine to the rostral incisure as rostrum and spine are easily damaged.

Fig. 4 *C. reticulata* ♀. A: Coxa of maxillula. B: Basale and endopodite of mandible. C: endopodite of maxillula. D: Sixth limb. E: Toothed edge of coxale and tooth lists of mandible. F: Fifth limb. G: Seventh limb.

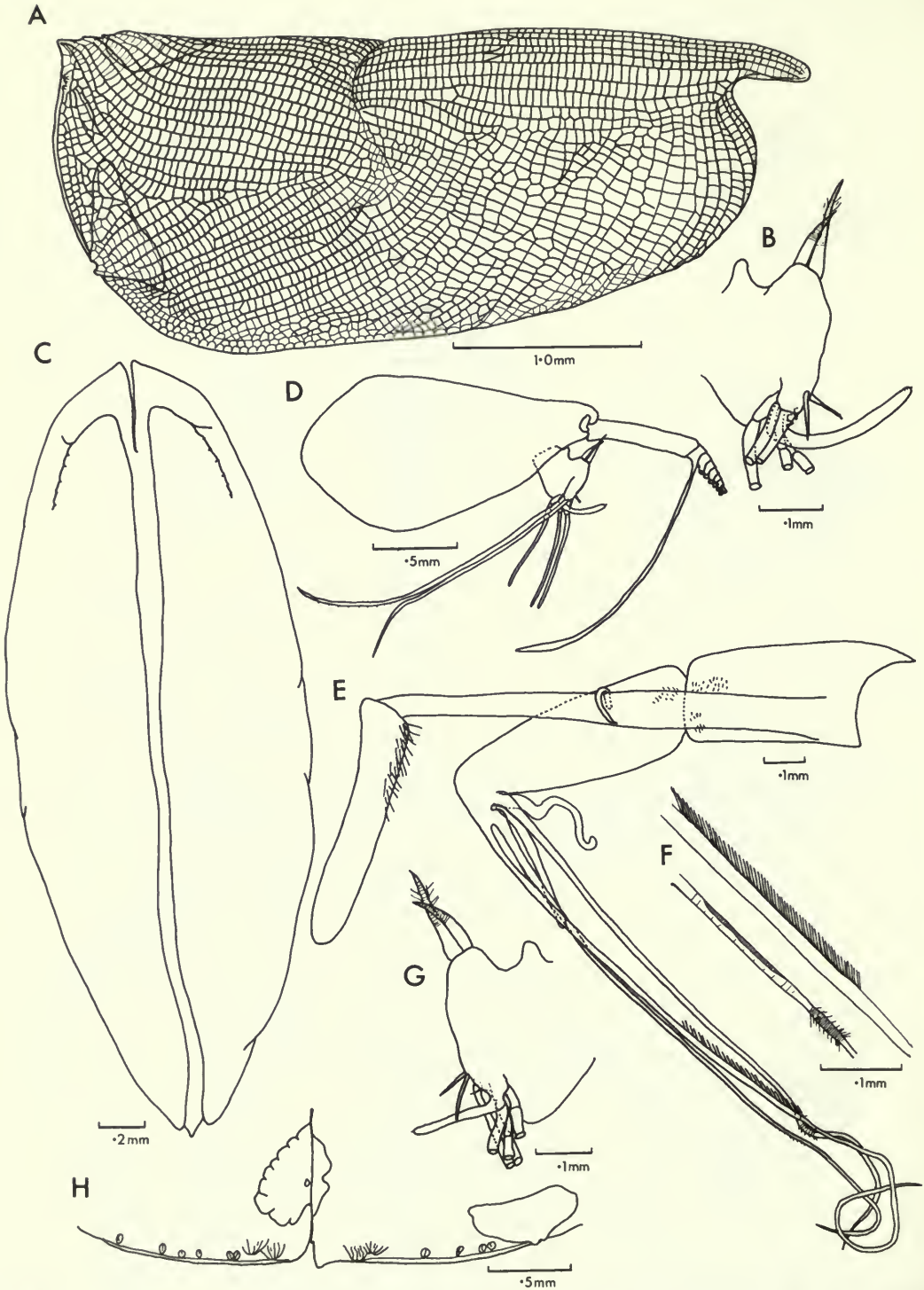

Fig. 5 *C. macroreticulata* ♂. A: Carapace, lateral view. B: Detail of the endopodite of the right second antenna. C: Ventral view of carapace. D: Second antenna. E: Frontal organ and first antenna. F: Detail of the *b* and *e* seta armatures. G: Detail of the endopodite of the second antenna. H: Detail of the posterior carapace glands.

Fig. 6 *C. macroreticulata* ♂. A: Coxa of maxillula. B: Basale and endopodite of mandible. C: Endopodite of maxillula. D: Toothed edge of coxale and tooth lists of mandible. E: Penis. F: Caudal furca. G: Toothed edge of labrum. H: Sixth limb. I: Seventh limb. J: Fifth limb.

Carapace (Figs 7A, C & F). The 28 female specimens and six detached carapaces of females showed a carapace length range of 3·8 mm to 4·4 mm averaging 4·14 mm. The shape and sculpturing of the carapace is like that of the male but the rostrum is much longer and tapered. The asymmetrical glands, paired glands and edge glands are similar in appearance and position to those of the male.

Frontal organ and first antenna (Fig. 7E). These are similar in proportions and armature to *C. reticulata.*

Second antenna (Figs 7B & D). The proportions of the protopodite, exopodites and longest swimming seta are equivalent to those in the *C. reticulata* female. On the basal article of the endopodite the *b* seta bears a few short bristles. The second endopodite article has a single fairly long spine as well as the usual two setae. No equivalent spine was seen in *C. reticulata.*

Other appendages (Figs 8A–G). These appear to be similar to *C. reticulata* females.

REMARKS. 74 specimens were identified from *Discovery* material all occurring in bathypelagic hauls at stations between 10°N and 31°N in the Atlantic. Besides the 34 females and 21 males there were 13 stage VI juveniles (2·8, 2·9, 3·0, 3·1, 3·1, 3·1, 3·1, 3·1, 3·1, 3·2, 3·2 and 3·2 mm) 4 stage V juveniles (2·1, 2·3, 2·4 and 2·4 mm) and two stage IV juveniles (1·3 and 1·5 mm). The limited data available suggests that the adults occur in depths between 2500 m and 3500 m, deeper than *C. reticulata* though the juveniles can be found at shallower levels.

The BM(NH) holds some material recorded as *C. reticulata,* registration number 1924.7.19.182–183, 'Gauss' station, Deutsche Südpolar-Expedition 1901–1903, S Atlantic (loc.) which was purchased from the Berlin Museum. The tube contains two adult *C. macroreticulata,* one male and one female, and a label stating 'Gaussexp' and the date '22.x.01'. Müller in his report of the Ostracoda of the Deutsche Südpolar Expedition (1909) gives details for the station worked on 22.x.01 as 23°33′S 16°59′W, fished to 3000 m over a sounding of 5045 m, but he does not record *C. reticulata* as occurring at this station, so there is an element of doubt that he was responsible for identification of this material. Furthermore the male measures 3·8 mnm, much larger than the size of 3·1 mm given by Müller for the male of *C. reticulata* in both his original description (1906) and in his later Das Tierrich (1912).

Conchoecia spinireticulata sp. nov.

Conchoecia reticulata Müller 1906 (*pro parte*). Ergeb. Tiefsee-Exp. **8**, p. 64 pl. 12 f. 10–17.
Conchoecia reticulata Müller 1912 (*pro parte*). Das Tierrich—Ostracoda Berlin p. 71.
Macroconchoecia reticulata (Müller) Granata & di Caporiacco 1949. Rés. Campagnes Scientifiques **109** p. 1–51.
Conchoecia reticulata Müller. G. B. Deevey 1968. Peabody Museum of Natural History, Yale University. Bull. **26** p. 38 fig. 13.
Paraconchoecia reticulata (Müller) E. M. Poulsen 1973. Dana Report 84, p. 31–35 f 12a–l.
Conchoecia sp. *aff. reticulata* Müller. M. V. Angel, 1979. Prog. Oceanog. **8**, p. 57–58.
Conchoecia reticulata Müller. G. B. Deevey & A. L. Brooks 1980. Bull. Florida State Mus. **26** (2) p. 76–80 fig. 17.
Conchoecia sp. *aff. C. reticulata* Müller. M. V. Angel 1981. Atlas del Zooplancton del Atlantico sudoccidental ed. D. Boltovskoy, p. 559 f 194–78.

Male

The holotype mounted on slides in Euparal and stained with lignin pink, has been deposited at the BM(NH) No. 1982: 178. It has a carapace length of 3·4 mm and was caught at *Discovery* station 7856 (30°13·6′N 23°01·9′W) haul 51 with the RMT 1.

Carapace (Figs 9A, C & H). The lengths of the 88 male specimens ranged between 2·8 mm and 3·4 mm averaging 3·2 mm. Carapace shape is similar to *C. reticulata.* The nature and position of the carapace glands are similar to *C. reticulata* though there are rather more edge glands along the posterior margin. The shoulder vaults are slightly enlarged and heavily armoured with spines. The spines are arranged in nearly horizontal rows in the anterior-

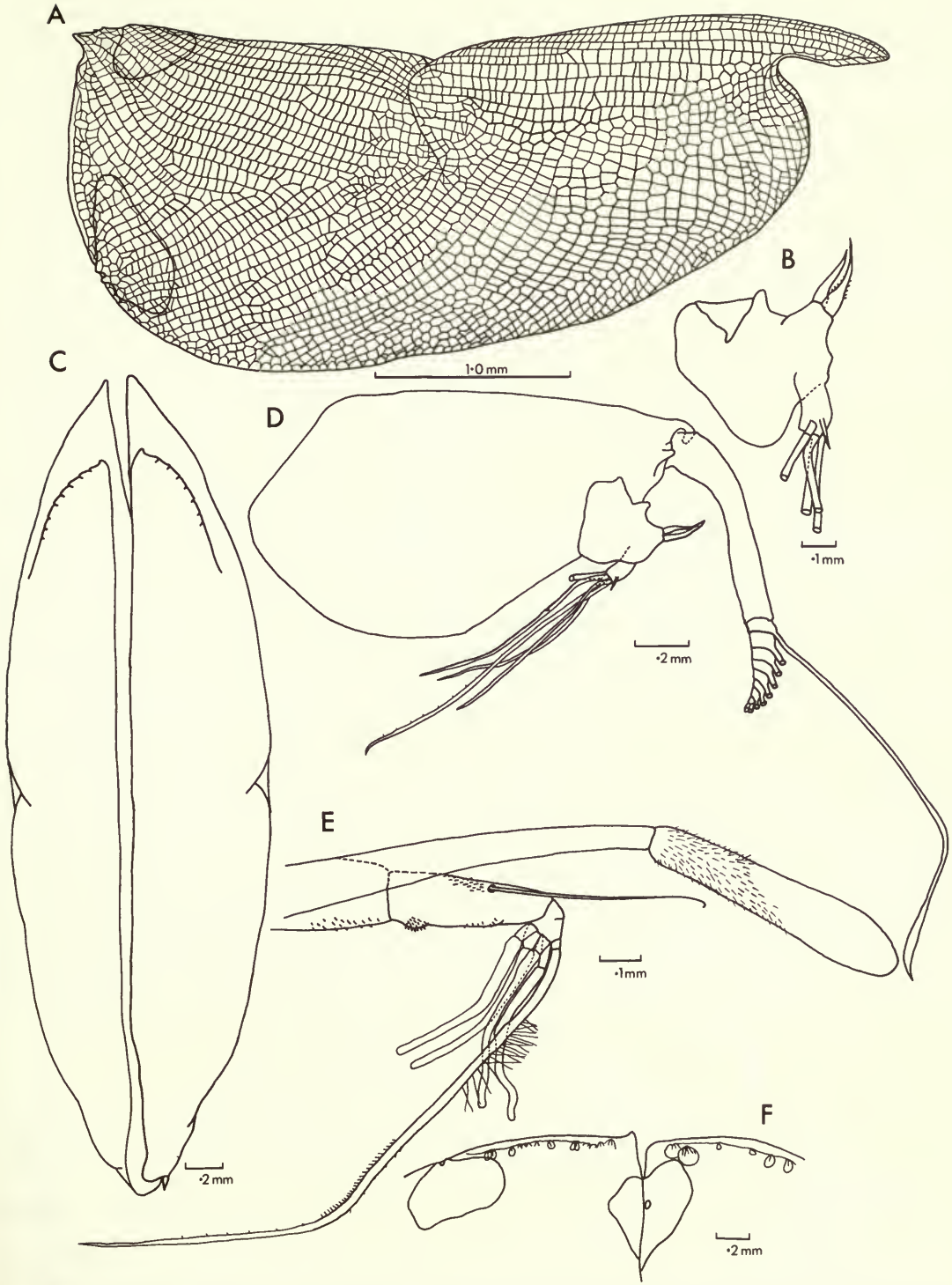

Fig. 7 *C. macroreticulata* ♀. A: Carapace, lateral view. B: Detail of endopodite of second antenna. C: Ventral view of carapace. D: Second antenna. E: Frontal organ and first antenna. F: Detail of the posterior carapace glands.

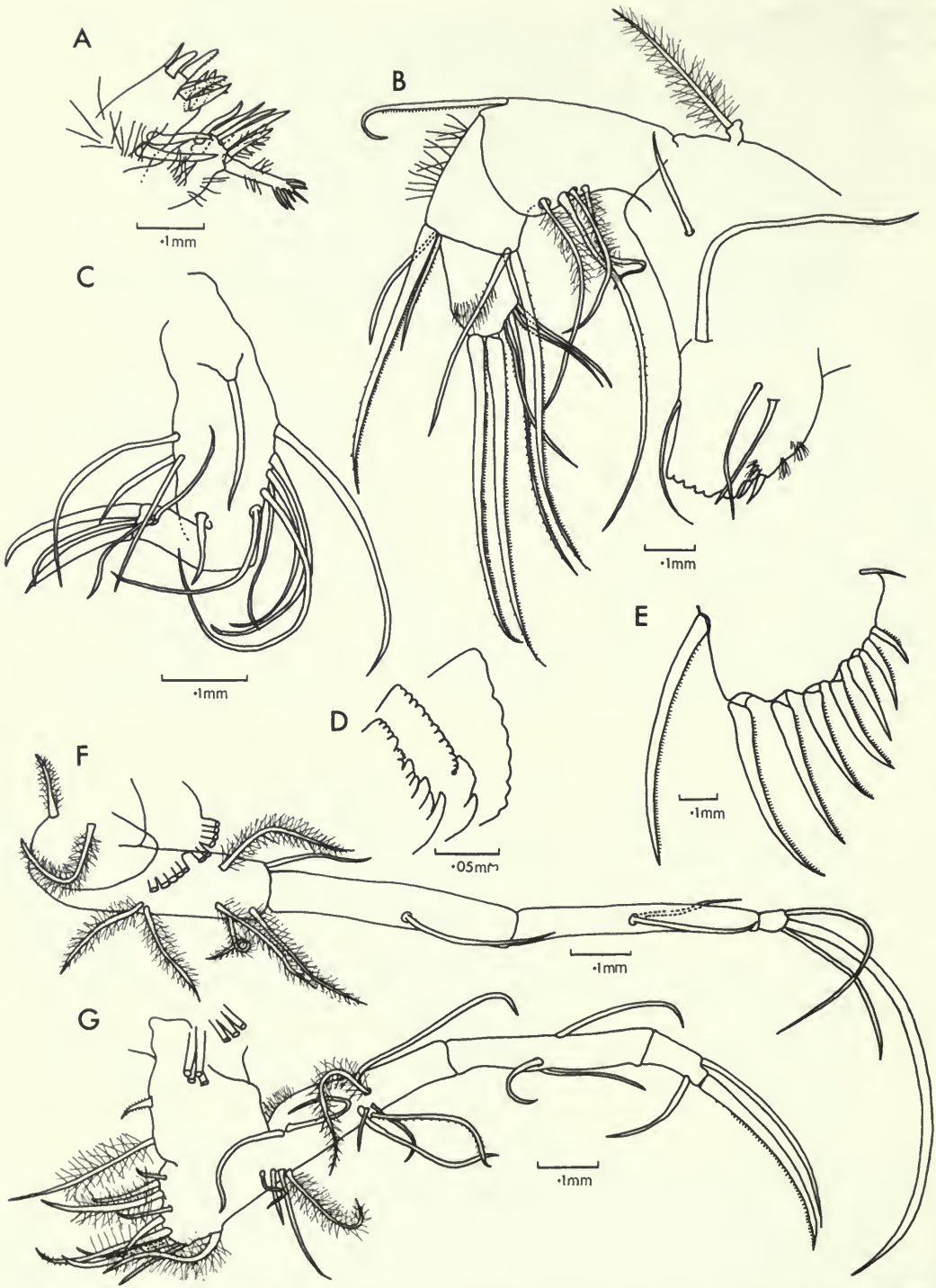

Fig. 8 *C. macroreticulata* ♀. A: Coxa of maxillula. B: Basale and endopodite of mandible. C: Endopodite of maxillula. D: Toothed edge of coxale and tooth lists of mandible. E: Caudal furca. F: Sixth limb. G: Fifth limb.

dorsal quarter. The ventral three rows have enlarged spines and curve into the notch behind the shoulder vaults. The more dorsal rows run across the top of the notch. In the posterior dorsal quarter there are parallel rows of narrow rectangles armoured with small spines along the near-horizontal lines. The posterior ventral quarter has similar sculpture with spines slanted diagonally downwards towards the back. In the anterior ventral quarter the sculpture is more squarrous and less well-marked. It is comparatively faint near the centre of the carapace and along the ventral and posterior margins.

Frontal organ (Fig. 9D). The proportions of the organ are similar to those of the previous species but the bristles on the capitulum are short.

First antenna (Figs 9D & E). The relative proportions of the setae differ from *C. reticulata* (Table 1). The *c* seta is a little shorter with the *b, d* and *e* setae longer. The armature of the *e* seta differs in having 83 pairs of spines rather than 50 pairs as in the previous species.

Second antenna (Figs 9B, F & G). As in *C. macroreticulata* the f, g and the longest swimming setae are relatively longer than in *C. reticulata.* The *b* seta on the endopodite lacks long bristles.

Penis (Fig. 10E). This differs from the previous species in having only four oblique muscle bands.

Other appendages (Fig. 10). These are similar to those of *C. reticulata.*

Female

The paratype specimen, carapace length 3·8 mm, stained with lignin pink and mounted on slides in Euparal, has been deposited at the BM(NH) No. 1982: 177. It was caught at *Discovery* station 7856 (30°03·7′N 23°00·2′W) haul 50 with the RMT 1.

Carapace (Figs 11A, B & F). The 80 female specimens ranged in length between 3·2 and 3·9 mm averaging 3·7 mm. Like the previous species, the features of the carapace are much like those of the male but the rostrum tapers more gradually and is longer.

Second antenna (Figs 11D & E). The proportions of the protopodite exopodites and longest swimming seta are equivalent to the previous species. As in *C. macroreticulata* and unlike *C. reticulata* the *b* seta of the endopodite has a few short bristles and the second article bears a single long spine.

Other appendages (Fig. 12). These are similar to those of *C. reticulata* females.

REMARKS. 626 specimens were identified from *Discovery* material, all at mesopelagic or deep mesopelagic depths from stations between 0°–32°N in the Atlantic. Besides the 88 males and 80 females there were 117 stage VI juveniles ranging in size from 2·4–3·0 mm, 188 stage V juveniles, 1·6–2·2 mm and 153 stage IV juveniles 1·1–1·5 mm. All the juvenile instars bore rows of spines on the carapace. The data from all stations have been combined and plotted in Fig. 13 to show the generalised depth distributions of the instars and adults. Stage IV instars were commonest between 600 m and 800 m, stage V between 700 m and 900 m, stage VI between 1000 m and 1250 m, adults between 1000 m and 2000 m. Ontogenetic migration into deeper water with age is common in many halocyprid species (Angel, 1979).

Conchoecia caudata Müller 1891

Conchoecia caudata G. W. Müller 1891. Zool. Jahrb. Syst. **5** p. 276 pl. 29 f 45–49.
Conchoecia caudata G. W. Müller 1906. Ergeb. Tiefsee-Exp. **8** p. 65 pl 11 f 24, pl. 12 f 1–9.
Conchoecia caudata G. W. Müller 1912. Das Tierrich—Ostracoda Berlin p. 71.
Paraconchoecia caudata E. M. Poulsen 1973. Dana Report 84 p. 35–42 fig. 13a–o.

Male

A male with a carapace length of 5·6 mm, measured from the tip of the left valve rostrum to the tip of the right valve posterior dorsal spine, stained with lignin pink and mounted on slides in Euparal has been deposited at the BM(NH) No. 1982: 192. It was caught in the Indian Ocean at *Discovery* station 5345 (16°58′S 67°31·1′E) with an Isaacs-Kidd Midwater Trawl (Foxton, 1969).

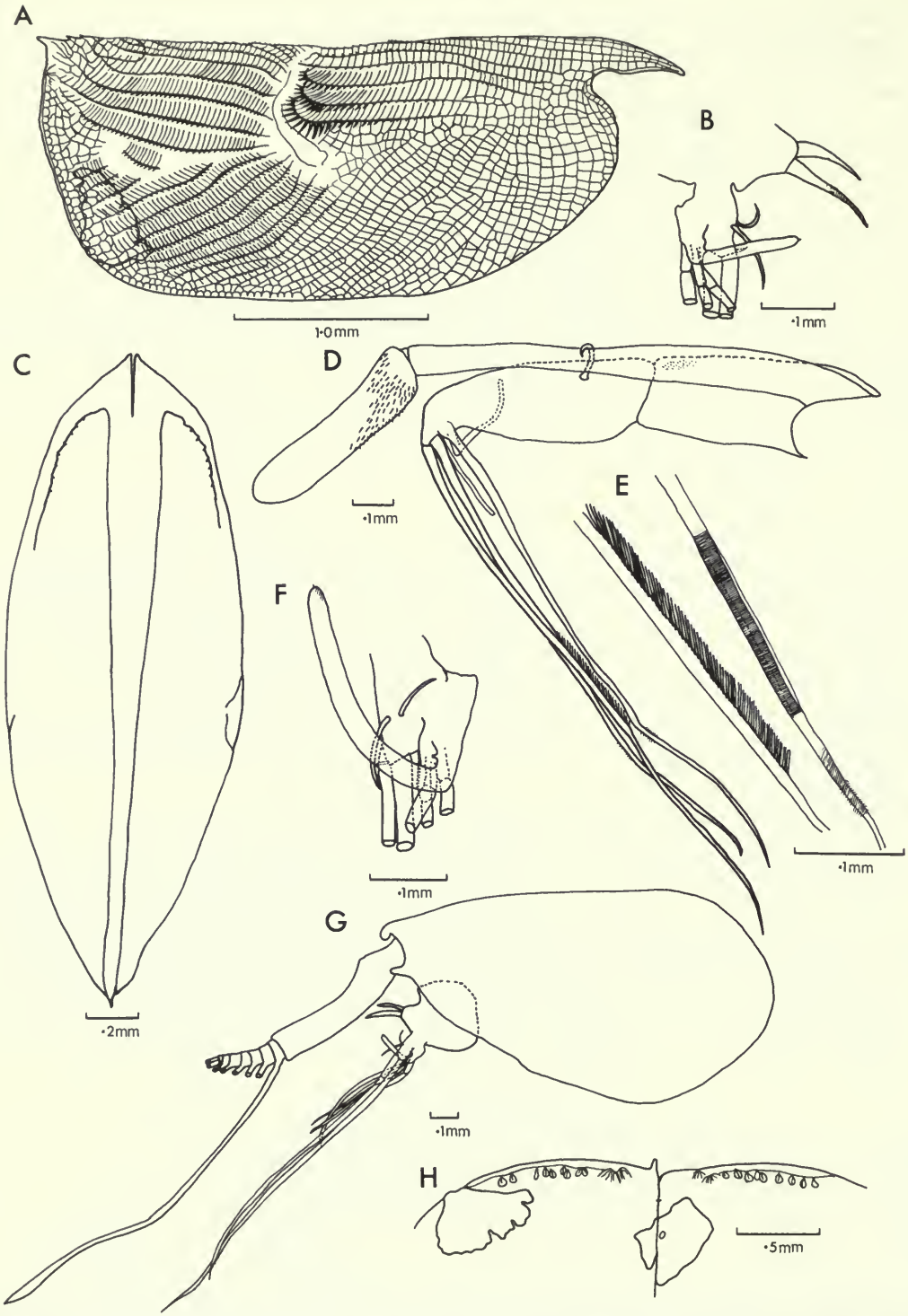

Fig. 9 *C. spinireticulata* ♂. A: Carapace, lateral view. B: Detail of endopodite of left second antenna. C: Ventral view of carapace. D: Frontal organ and first antenna. E: Detail of *b* and *e* seta armatures. F: Detail of endopodite of right second antenna. G: Second antenna. H: Detail of the posterior carapace glands.

Fig. 10 *C. spinireticulata* ♂. A: Toothed edge of labrum. B: Basale and endopodite of mandible. C: Coxa of maxillula. D: Endopodite of maxillula. E: Penis. F: Caudal furca. G: Sixth limb. H: Fifth limb. I: Toothed edge of coxale and tooth lists of mandible.

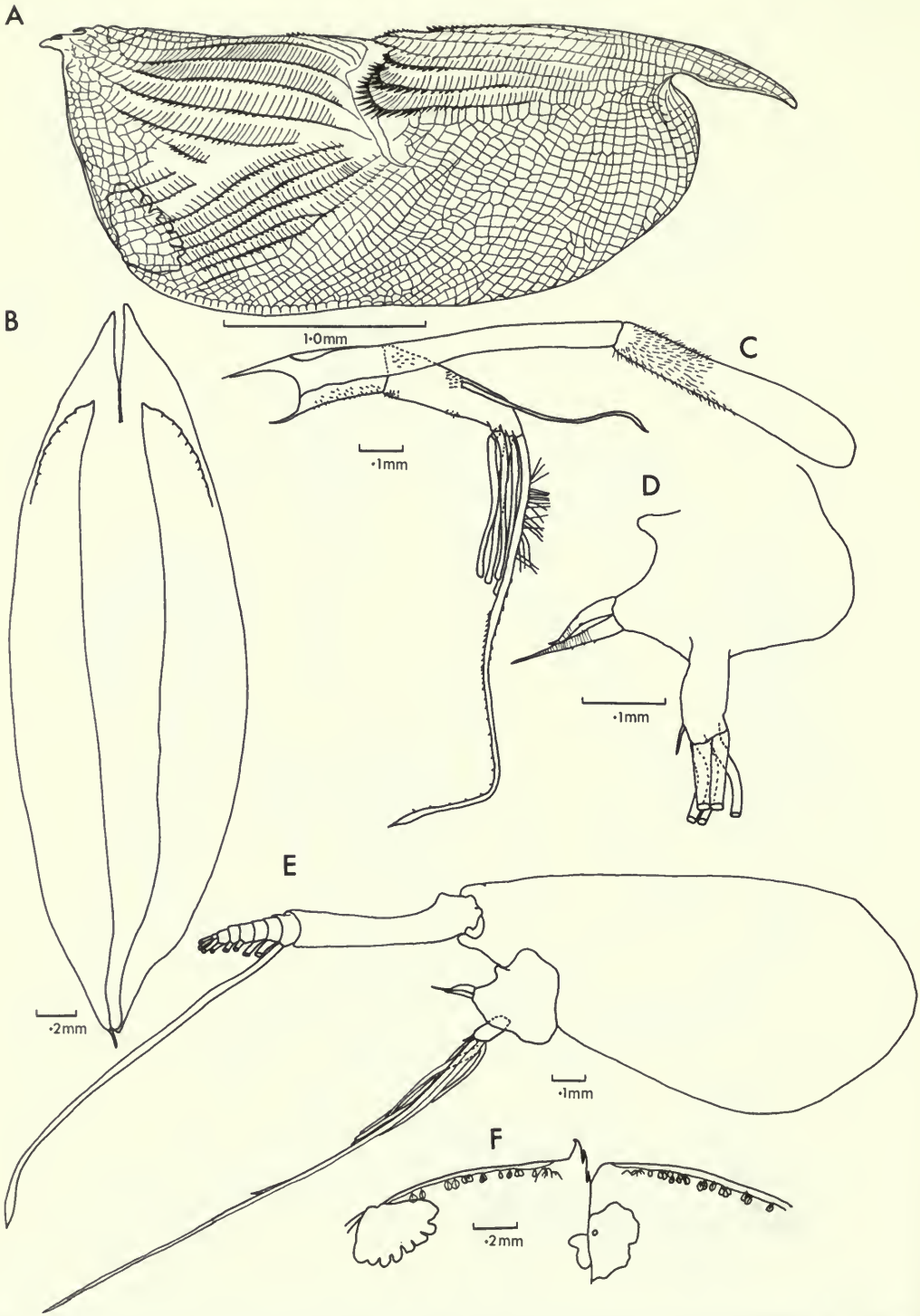

Fig. 11 *C. spinireticulata* ♀. A: Carapace, lateral view. B: Ventral view of carapace. C: Frontal organ and first antenna. D: Detail of endopodite of second antenna. E: Second antenna. F: Detail of the posterior carapace glands.

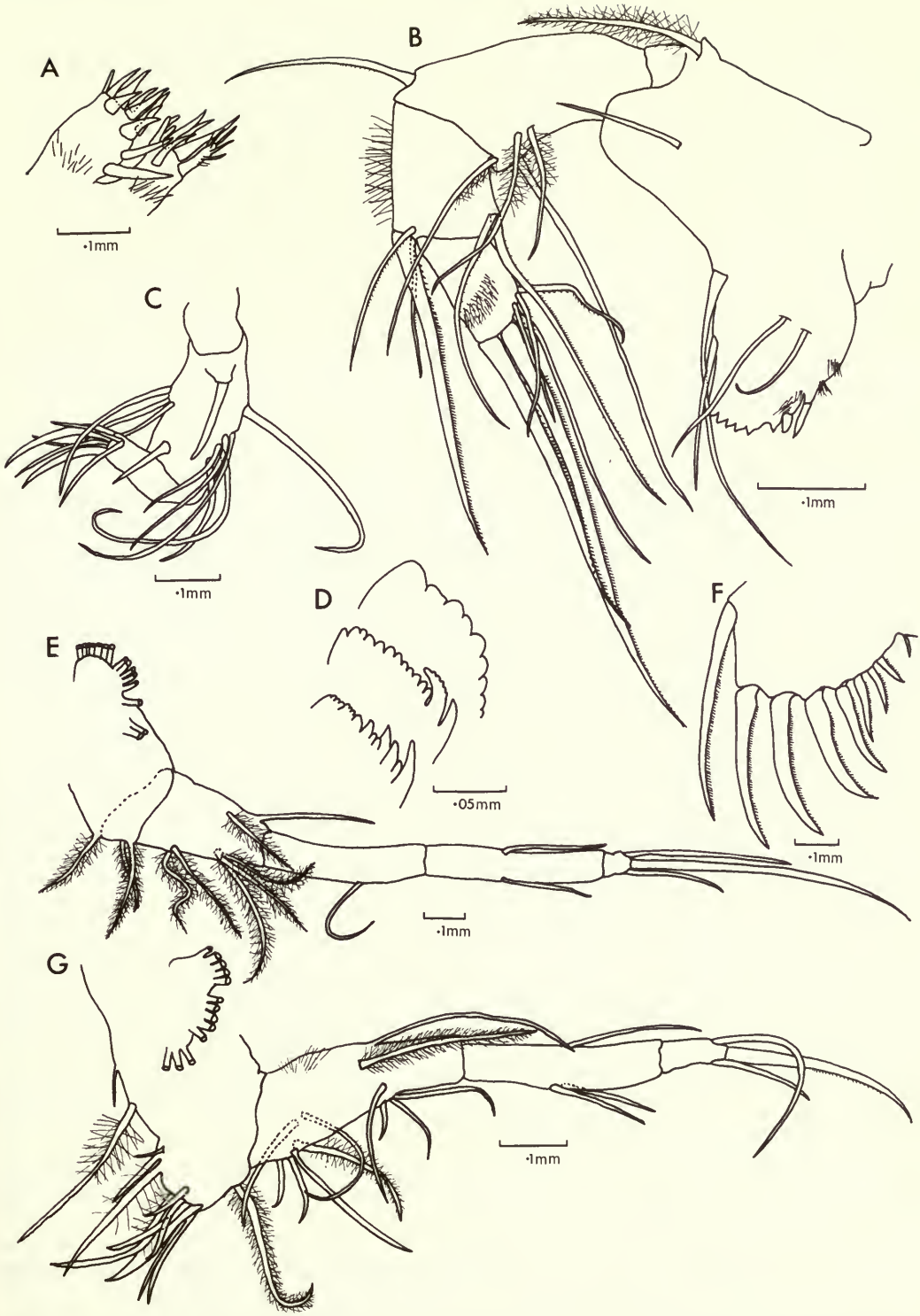

Fig. 12 *C. spinireticulata* ♀. A: Coxa of maxillula. B: Basale and endopodite of mandible. C: Endopodite of maxillula. D: Toothed edge of coxale and tooth lists of mandible. E: Sixth limb. F: Caudal furca. G: Fifth limb.

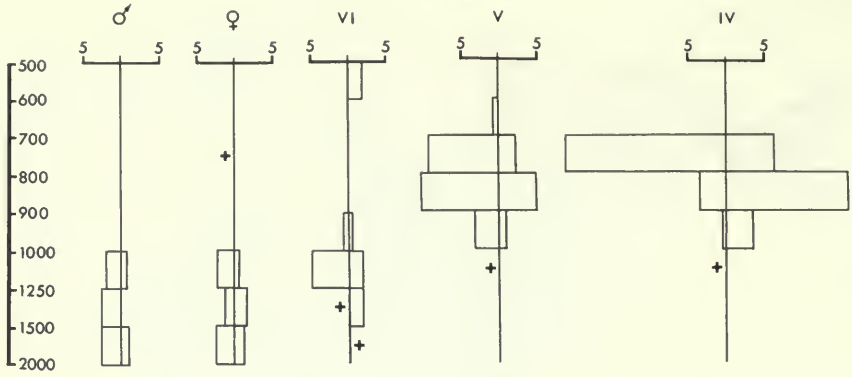

Fig. 13 Vertical profiles of density of *C. spinireticulata* (numbers per 2 hour tow) of males, females and juveniles (stages VI, V & IV) by day (on left) and by night (on right). Data combined from all stations. + indicates presence in densities of less than 0·5 per 2 hr tow.

Carapace (Figs 14A, C & H). The size of the five males, averaging 5·61 mm, none significantly damaged, were 4·8 mm, 5·6 mm, 5·6 mm, 6·0 mm and 6·1 mm, an unusually wide range which may prove indicative of two size forms. The posterior dorsal corner of the left valve is drawn out into a short spine, whilst that of the right valve is produced into a long laterally-flattened spine which bears dorsal and ventral secondary spines. Near the base of the primary spine the ventral secondary spines are much smaller than the opposite dorsal ones but distally they are of more equal size. The left asymmetrical gland opens on a bump just anterior to the hinge. The posterior margin is curved and slopes anteriorly. Midway, on both valves, are prominent glands which open on the exhalent siphon and may be bioluminescent glands. These are flanked by a number of edge glands. The right asymmetrical gland opens just dorsal to the strongly curved posterior ventral corner. The rostrum is particularly elongate and tapers narrowly, that of the left valve is longer than the right. Glandular cells are present both in the rostrum and the long spine, these could be bioluminescent.

The sculpture resembles that of *C. spinireticulata.* In the posterior quarter there are five parallel rows of spines, the most ventral of which is short. These slope slightly upwards towards the back, but do not meet the dorsal hinge. Faint narrowly-spaced lines run at right-angles to these lines. In the posterior ventral quarter there are two short parallel rows of spines which slope downwards towards the back. Over the slightly expanded shoulder vaults the sculpture runs parallel to the dorsal hinge. The four bottom lines are armoured with spines. The top row of spines is straight but the bottom three rows curve over the posterior part of the shoulder vaults, at which point the spines are particularly long, and end in the notch. In the anterior ventral quarter the sculpture consists of faint squares or polygons, with the ventral corners drawn out into spines which get longer closer to the ventral margin. Along the ventral margin the spines are quite long and extend beyond the edge.

Frontal organ (Fig. 14B). The shaft reaches level with the end of the second segment of the first antenna. The capitulum, slightly narrowed in the distal half, has lateral bands of hairs with a few scattered dorsally and ventrally.

First antenna (Figs 14B & D). The main differences in the details of this appendage compared to *C. spinireticulata* are that there are about 95 pairs of spines on the *e* seta, and the callus on the *b* seta is relatively short and compact.

Other appendages (Figs 15A–I). These are all similar to those of *C. spinireticulata* with the exceptions of the single outer-face seta of the first segment of the mandibular endopodite, which has a row of short bristles, and the five oblique muscle bands of the penis.

Female

A female specimen, carapace length 6·7 mm, stained with lignin pink and mounted on slides

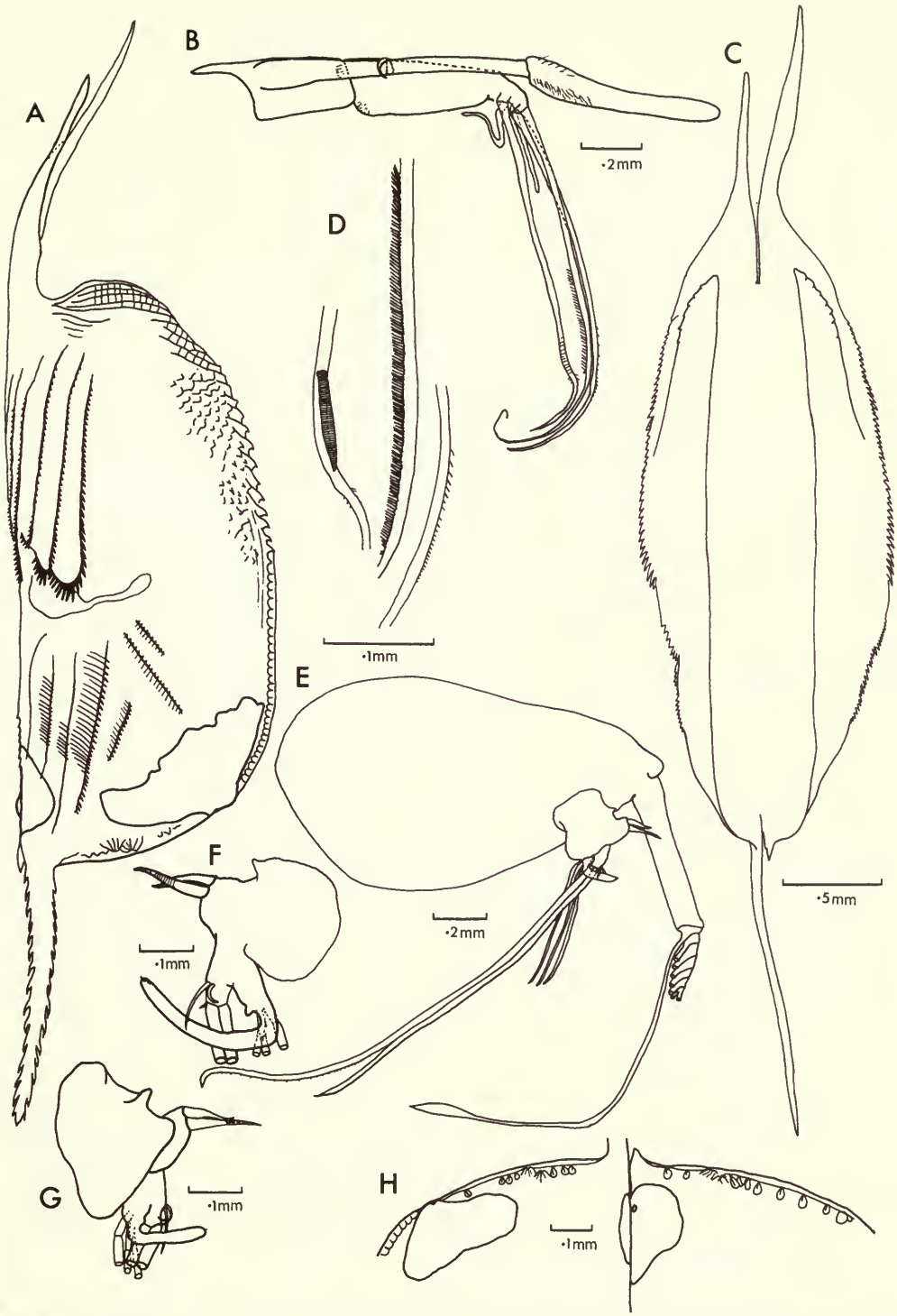

Fig. 14 *C. caudata* ♂. A: Carapace, lateral view. B: Frontal organ and first antenna. C: Ventral view of carapace. D: detail of the *b, d* and *e* setae armatures. E: Second antenna. F: Detail of endopodite of right second antenna. G: Detail of endopodite of left second antenna. H: Detail of posterior carapace glands.

Fig. 15 *C. caudata* ♂. A: Caudal furca. B: Basale and endopodite of mandible. C: Endopodite of maxillula. D: Toothed edge of labrum. E: Toothed edge of coxale and tooth lists of mandible. F: Penis. G: Fifth limb. H: Sixth limb. I: Coxa of maxillula.

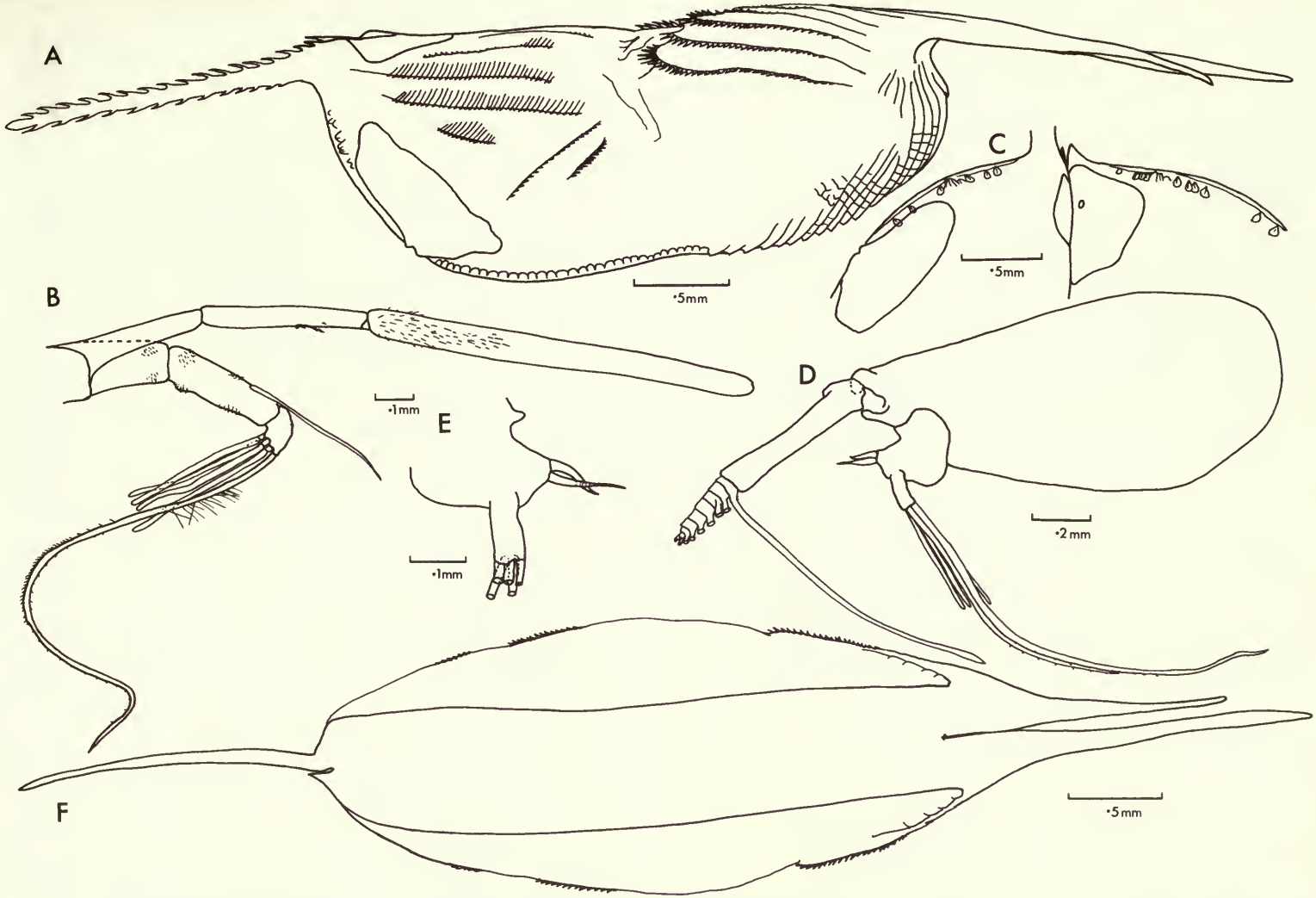

Fig. 16 *C. caudata* ♀. A: Carapace, lateral view. B: Frontal organ and first antenna. C: Detail of posterior carapace glands. D: Second antenna. E: Detail of endopodite of second antenna. F: Ventral view of carapace.

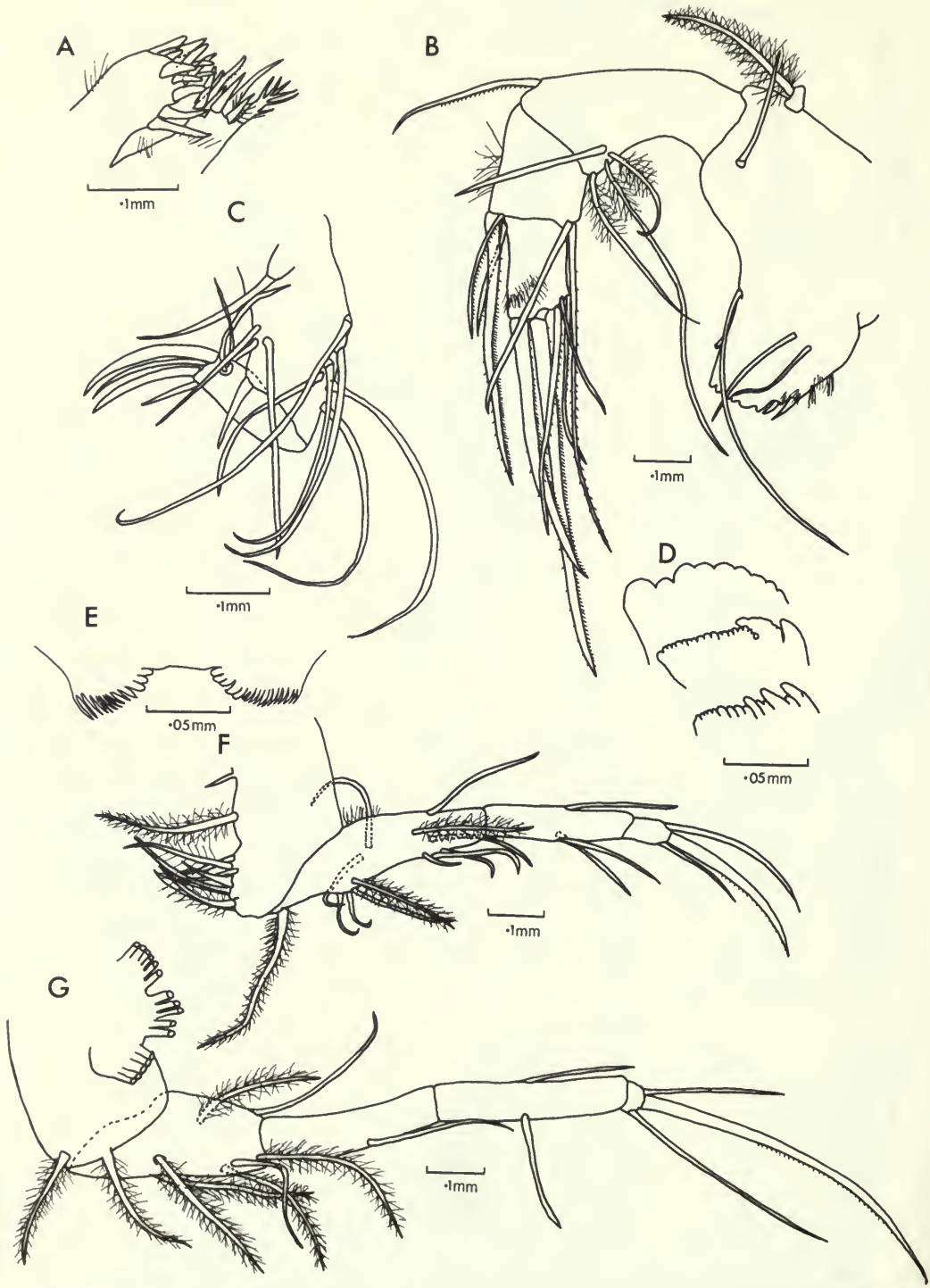

Fig. 17 *C. caudata* ♀. A: Coxa of maxillula. B: Basale and endopodite of mandible. C: Endopodite of maxillula. D: Toothed edge of coxale and tooth lists of mandible. E: Toothed edge of labrum. F: Fifth limb. G: Sixth limb.

in Euparal has been deposited at the BM(NH) No. 1982: 191. It was caught in the same haul as the male.

Carapace (Figs 16A, C & F). Of the eight females caught, one had a badly damaged posterior dorsal corner spine. The other seven ranged in size from 6·7 mm to 7·6 mm averaging 7·18 mm. The details of the shape sculpture and glands are similar to those of the male.

Frontal organ (Fig. 16B). The capitulum is narrow and exceptionally elongate with short spines on the proximal half.

Second antenna (Figs 16D & E). Unlike *C. spinireticulata* the second article of the endopodite lacks a spine.

Other appendages (Fig. 17). These appear to be similar in all respects to *C. spinireticulata* females.

Remarks. 17 specimens of *C. caudata* were identified from *Discovery* material from the Indian Ocean. Besides the five males and eight females there were three stage VI juveniles (6·4 mm, 6·0 mm, 5·6 mm) and one stage V juvenile (4·9 mm). There was too little material available to comment on the depth distribution of the species.

It appears to be an Indo-Pacific species, absent from the Atlantic. Although Müller (1906) recorded it from two Atlantic stations, 55 Vb, near 2°N 3°E and 91V near 33°S 16°E. This may be a mistake as it has not been found in *Discovery* Atlantic material (Angel, pers. comm.), Poulsen did not record it in either his *Dana* Report (1973) or his paper on the Ostracoda of the eastern tropical Atlantic (1969), nor Deevey in collections from the Sargasso Sea (1968, 1980), Caribbean (1970) and SW Atlantic (1974).

Discussion

In 1906 Müller placed *C. caudata* and *C. reticulata* in his *Spinifera* group of *Conchoecia* species which he characterised by the spine at the posterior dorsal corner of the right valve, long thin hairs proximally on the anterior surface of the female principal seta, the posterior margin of the mid part of the male principal seta equipped with long proximally-pointing, bristle-like close-set spines and distal to these a group of distally-directed spines, distinctive *b* and *d* setae armature and no lateral glands. This group included *C. spinifera, C. oblonga, C. allotherium, C. aequiseta, C. hirsuta, C. inermis, C. dasyophthalma, C. dorsotuberculata, C. echinata* and *C. mamillata* as well as *C. caudata* and *C. reticulata.* The grouping of these species has been criticised by both Skogsberg (1920) and Poulsen (1973) who pointed out the inconsistencies resulting from juxtaposing these undoubtedly heterogeneous species.

Nevertheless, *C. caudata, C. reticulata, C. macroreticulata* and *C. spinireticulata* all exhibit the characters outlined by Müller for the *Spinifera* group, with the exception that *C. caudata* is the only one of the four species with distally directed spines on the male principal seta. The four species themselves are clearly closely related having in common the comparatively few small edge glands along the posterior margin, paired glands in both sexes, bristles on the frontal organ in the male, cylindrical frontal organ in the female, short bristles on the posterior margin of the mid-section of the female principal seta and a wing-like callus on the *b* seta of the male first antenna alongside short bristles on the *d* seta.

The carapace, frontal organ and first antenna of the other species of Müller's *Spinifera* group were examined to see if any shared these additional *Reticulata* group characters. It was found that though none of the other species fitted into this category, *C. spinifera, C. oblonga* and *C. allotherium* form an equivalently close-knit group. They have in common many edge glands, paired glands in the males only, no bristles on the male frontal organ, a distinctively shaped and sharp pointed tip to the female frontal organ, long stiff bristles on the posterior margin mid-section of the female principal seta, approximately 30 pairs of proximally-pointing spines of the male principal seta are large robust and wider-spaced, distal to them is a single distally directed leaf-like spine, the *d* seta lacks armature and the *b* seta lacks a wing-like callus. Of the other species, *C. aequiseta* and *C. hirsuta,* which differs from *C. aequiseta* in only minor details of the appendages and distribution (Angel, pers.

comm.), *C. echinata, C. dorsotuberculata* and *C. inermis* have various combinations of characters which indicate affinity with the *Reticulata* and *Oblonga* groups, whilst each species has unique features. These species serve to underline the problems inherent in attempting to split up the massive genus *Conchoecia* into subgenera or genera. The three other *Spinifera* group species *C. dasyophthalma, C. mamillata* and *C. nanomamillata* share few common characteristics with any of the other species and there seems little basis for suggesting any particular affinity.

Within the *Reticulata* group the carapace details point to greater affinity of *C. macroreticulata* with *C. reticulata* and *C. caudata* with *C. spinireticulata* similarities which are emphasised by the few appendage distinctions. Thus *C. spinireticulata* and *C. caudata* have no hairs on the *b* seta of the male second antenna endopodite, which *C. reticulata* and *C. macroreticulata* have, the hairs on the male frontal organ are not so long as in *C. macroreticulata* and *C. reticulata* and the numbers of pairs of spines on the male principal seta are broadly equivalent in these pairs of species.

Key to the species of the *Reticulata* group

1. (i) Carapace sculpture armoured with rows of spines which are especially pronounced on the shoulder vaults and in the posterior dorsal region. In the ♂ there are no hairs on the *b* seta of the second antenna and there are between 80–100 pairs of bristles on the principle seta 2

   (ii) Carapace not armoured with such spines though in one species there are some small spines along the ventral margin. In the ♂ the *b* seta of the second antenna bears hairs, the frontal organ has relatively long hairs and there are about 50 pairs of bristles on the principal seta 3

2. (i) The posterior dorsal corner (PDC) of both valves are drawn out into spines, that of the left valve is fairly short and that of the right valve is exceptionally long and it is about 25% of the total carapace length. The rostrum is similarly elongate and is slightly longer on the left valve than on the right. The paired glands are situated about half way down the posterior margin. ♀ 6·75–7·6 mm ♂ 4·82–6·12 mm (lengths inclusive of spine and rostrum) ..... ***C. caudata***

   (ii) The PDC of the right valve is drawn out into a spine whereas that of the left valve is rounded. Neither the spine nor the rostrum are particularly extended. The paired glands are situated just ventral to the PDC. ♀ 3·2–3·9 mm ♂ 2·8–3·4 mm ..... ***C. spinireticulata***

3. (i) Carapace with small spines projecting from the ventral margin especially on the left valve. The ventral margin, in the central section is nearly parallel to the dorsal hinge. In the posterior dorsal region the rows of sculpture are nearly horizontal ♀ 3·2–3·4 mm ♂ 2·8–3·1 mm ..... ***C. reticulata***

   (ii) Carapace tapers anteriorly and the ventral edge of the carapace lacks spines. The rows of sculpture, in the posterior dorsal region, slant dorsally. ♀ 3·8–4·4 mm ♂ 3·4–4·0 mm ..... ***C. macroreticulata***

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The juvenile stages of eight swimming crab species (Crustacea: Brachyura: Portunidae); a comparative study

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Introduction

The comparative larval morphology of many brachyuran crabs occurring in N Atlantic waters has become better known during the last two decades (see Rice, 1980 for references). However, except for the studies by Lebour (1928), early post-larval stages have not been investigated comparatively to facilitate identifications of young crabs that frequently occur in intertidal and benthic samples. The availability of reared material together with recent rich hauls of juvenile crabs obtained from the Porcupine Sea Bight has prompted this comparative study of the early crab stages of eight swimming crab species all belonging to the family Portunidae and to the sub-family Polybiinae.

Crabs described here are: (1) *Liocarcinus arcuatus* (Leach); (2) *L. pusillus* (Leach); (3) *L. depurator* (Linnaeus); (4) *L. puber* (Linnaeus); (5) *L. holsatus* (Fabricius); (6) *Macropipus tuberculatus* (Roux); (7) *Bathynectes longipes* (Risso); (8) *Polybius henslowii* Leach.

The crab stages (1)–(5) are figured chiefly from material reared in the larval rearing laboratory of the British Museum (Natural History) during the past ten years and as a part of the ongoing studies on NE Atlantic brachyuran crabs. Specimens representing species (6) and (7) were collected during RRS *Discovery* Cruise 105 (1979) while the material of species (8) is from the collections of the *Michael Sars* North Atlantic Deep-Sea Expedition (1910).

Measurements: carapace length (cl) = distance between mid-line frontal and posterior margin of carapace; carapace width (cw) = distance from tip to tip of longest pair of anterio-lateral spines.

Descriptions

(1) *Liocarcinus arcuatus* (Leach)

Portunus arcuatus, Lebour 1928: 510, Pl. VII, fig. 2 (1st–6th crab).

MATERIAL EXAMINED. Reared from ♀ collected at Kylesalia, Galway Bay, Ireland, 2.vii.1982, 1st crab–5 spms 1·5–1·7 mm cl., BM(NH) reg. no. 1983: 16, colld P. F. Clark.

Only the FIRST CRAB was obtained. Carapace (Fig. 1a) as long as broad; front slightly less than $\frac{1}{2}$ carapace width, median lobe small, deflected ventrally and obtuse; orbital dorsal margin forming a very broad even curve. Two prominent anterio-lateral teeth; 1st not developed; 2nd represented as a minute, acute lobe; 3rd large, narrow, curved and acute; 4th not developed; 5th small, curved forward and acute.

Pereiopods 2–4 relatively thin; merus of 4th (Fig. 3a) length slightly exceeding 5× width, dactylus thin, styliform and straight throughout its length. Pereiopod 5 (Fig. 4a) dactylus narrow, length almost $5\frac{1}{2}\times$ maximum width.

(2) *Liocarcinus pusillus* (Leach)

Portunus puber, Williamson 1911: Pl. III, fig. 29; *Portunus pusillus,* Lebour 1928: 512, Pl. VII, fig. 1 (1st–6th crab).

MATERIAL EXAMINED: Reared from ♀ collected off Langness Point, Isle of Man, 23.vii.1975, 1st crab–5 spms 1·9–2·0 mm cl., BM(NH) reg. no. 1976: 249, colld A. A. Fincham. Deep Point, Scilly Isles, 33 m, 13.vii. 1964, 2nd crab–1 spm 2·3 mm cl., BM(NH) reg. no. 1968: 589; same locality, 14.vii.1966, 4th ? crab–1 spm 3·1 mm cl., BM(NH) reg. no. 1968: 475, colld BM(NH) and London University Sub-aqua Exped., Scilly Isles.

FIRST CRAB. Carapace (Fig. 1b) slightly longer than broad; front slightly less than $\frac{1}{2}$ carapace width, median lobe broadly rounded; orbital dorsal margin forming an angular curve. Two prominent, forwardly curved anterio-lateral teeth; 1st obtuse; 2nd represented as a minute, obtuse lobe; 3rd large, stout and acute; 4th forming a small sub-acute lobe; 5th large and acute.

Pereiopods 2–4 moderately stout; merus of 4th (Fig. 3b) length about $4\frac{3}{4}\times$ width, dactylus styliform and curved, noticeably shorter than merus. Pereiopod 5 (Fig. 4b), dactylus moderately broadened proximally, length about $4\frac{3}{4}\times$ maximum width.

LATER STAGES. Anterio-lateral teeth of carapace of 2nd crab similar to 1st stage. In 4th stage (Fig. 1c) all 5 teeth developed but 2nd and 4th less pronounced than others.

(3) *Liocarcinus depurator* (Linnaeus)

? *Portunus holsatus,* Williamson 1911: Pl. II, figs 13, 13a (1st crab); *Portunus depurator,* Björck 1913: 26, Taf. figs 5, 6 (1st crab); Lebour 1928: 515, Pl. VI, fig. 1 (1st–5th crab).

MATERIAL EXAMINED. Reared from ♀ collected in Strangford Lough, Co. Down, Ireland, 14.iv.1976, 1st crab–5 spms 2·1–2·5 mm cl., 2nd crab–5 spms 2·9–3·2 mm cl., BM(NH) reg. no. 1983: 17, colld A. A. Fincham.

FIRST CRAB. Carapace (Fig. 1d) broader than long; front less than $\frac{1}{2}$ carapace width, median and submedian lobes broad, inconspicuous and slightly emarginate; orbital dorsal margin strongly angular. Three prominent, forwardly curved anterio-lateral teeth; 1st broad and obtuse; 2nd represented as a small obtuse lobe; 3rd large, stout and acute; 4th small and acute; 5th large and acute.

Pereiopods 2–4 moderately stout; merus of 4th (Fig. 3b) length about $4\frac{1}{4}\times$ width, dactylus stout, terminally curved and almost as long as merus. Pereiopod 5 (Fig. 4c) dorsal margin of merus serrate, dactylus moderately broadened, length slightly exceeding $3\frac{1}{2}\times$ maximum width.

LATER STAGES. 2nd crab (Fig. 1e) with all 5 anterio-lateral teeth conspicuous; 2nd angular; 4th rather stouter than 5th, curved and acute.

(4) *Liocarcinus puber* (Linnaeus)

Portunus puber, Lebour 1928: 508, Pl. V, figs 3, 4 (1st–5th crab).

MATERIAL EXAMINED. Reared from ♀♀ collected from Lulworth Cove, Dorset, Sept. 1972, BM(NH) reg. no. 1974: 334, colld Guildford Sub-aqua Club and from near Plymouth, Devon, May 1973, colld Mar. Biol. Lab. Plymouth, 1st crab–5 spms 2·2–2·5 mm cl., 2nd crab–3 spms 3·0 mm cl., 3rd crab–5 spms 3·5–3·7 cl., 4th crab–1 spm 4·0 mm cl.

FIRST CRAB. Carapace (Fig. 1f) broader than long; front less than $\frac{1}{2}$ carapace width and faintly granular to denticulate, median lobe not developed; orbital dorsal margin forming a broad and regular curve. Three prominent anterio-lateral teeth; 1st large, stout and acute; 2nd represented by an obtuse lobe; 3rd stout, projecting outwards and acute; 4th just discernible as an obtuse projection; 5th small, stout, acute and projecting forward.

Pereiopods 2–4 moderately stout; merus of 4th (Fig. 3d) length almost $4\times$ width, dactylus noticeably stout and styliform, slightly curved at apex. Pereiopod 5 (Fig. 4d), dactylus slightly broadened, length about $5\times$ maximum width, terminally very acute.

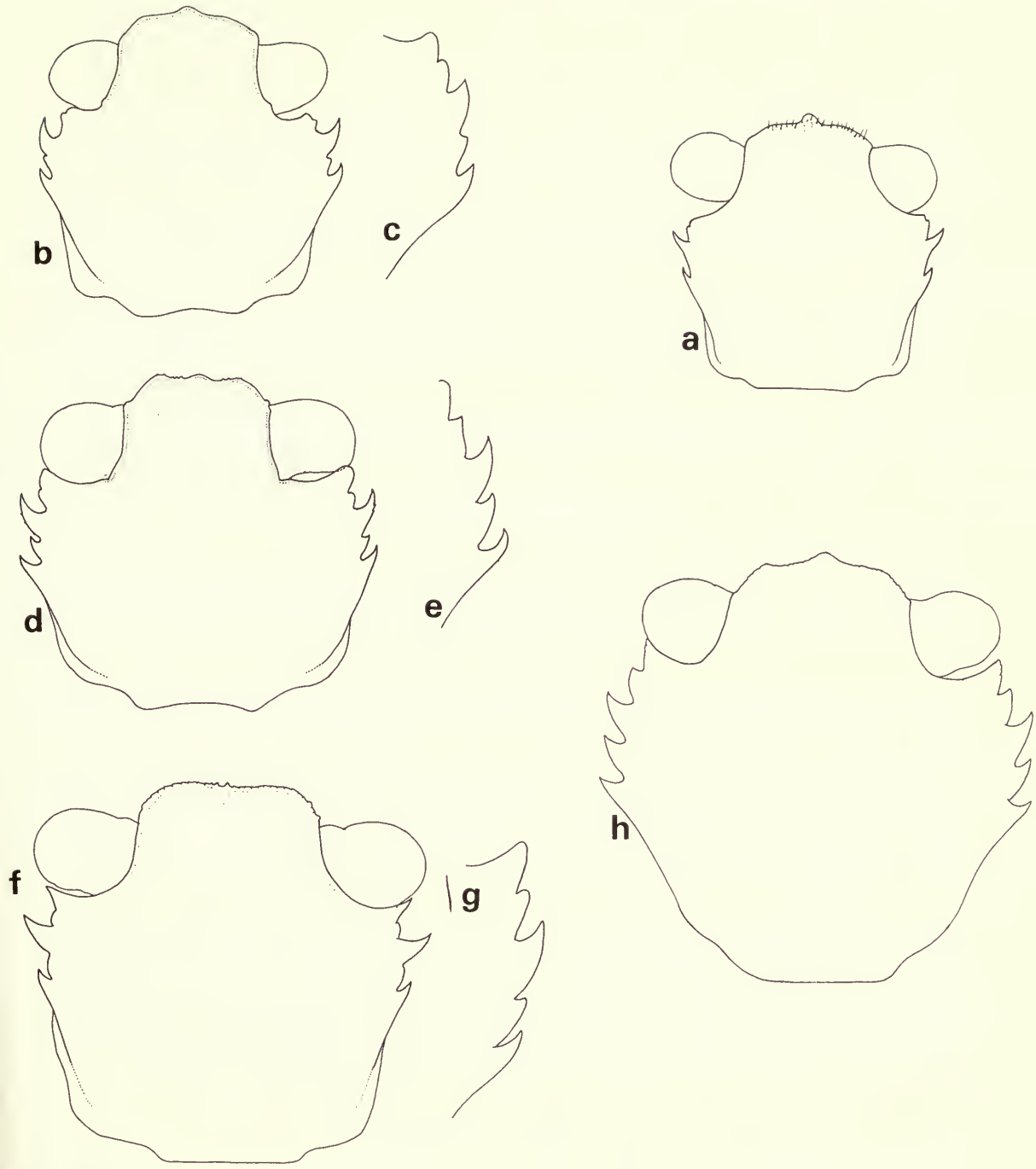

Fig. 1 a, b, d, f, h, outline dorsal aspects of carapace; c, e, g, anterio-lateral teeth of right side: a, *Liocarcinus arcuatus,* 1st crab 1·7 mm cl; b, *L. pusillus,* 1st crab 1·9 mm cl; c, 4th crab 3·1 mm cl; d, *L. depurator,* 2·1 mm cl; e, 2nd crab 3·0 mm cl; f, *L. puber,* 1st crab 2·2 mm cl; g, 4th crab 4 mm cl; h *L. holsatus,* 1st crab 2·6 mm cl.

LATER STAGES. Anterio-lateral teeth of carapace of 2nd crab similar to 1st stage. In 4th stage (Fig. 1g) 2nd and 4th teeth prominent but obtuse.

(5) *Liocarcinus holsatus* (Fabricius)

Portunus holsatus, Lebour 1928: 514, Pl. VI, fig. 2 (1st–4th crab).

MATERIAL EXAMINED. Reared from ♀ collected in Port Erin region, Isle of Man, Feb. 1973, 1st crab–5 spms 2·8–3·1 mm cl., BM(NH) reg. no. 1974: 333, colld Mar. Biol. Lab. Port Erin. Same locality, Feb. 1979, 1st crab–5 spms 2·7 mm cl., BM(NH) reg. no. 1983: 19, colld J. Ellis and P. F. Clark.

FIRST CRAB. Carapace (Fig. 1h) almost as broad as long; front less than $\frac{1}{2}$ carapace width, median lobe prominent; orbital dorsal margin forming a more or less even curve, somewhat angular. Five prominent anterio-lateral teeth, all acute; 2nd smallest; 3rd largest; 5th directed outward.

Pereiopods 2–4 moderately stout; merus of 4th (Fig. 3e) margins serrate; length about $3\frac{3}{4}\times$ width, dactylus thin, styliform and evenly curved. Pereiopod 5 (Fig. 4e), merus about as long as propodus, dactylus moderately broadened, distally acute to subacute, length about $3\frac{1}{2}\times$ maximum width.

LATER STAGES. The anterio-lateral teeth of the 2nd crab stage are slightly more accentuated than in the 1st stage and from the 3rd stage resemble those of the adult form.

(6) *Macropipus tuberculatus* (Roux)

Larvae and post-larval stages unknown.

MATERIAL EXAMINED. *Discovery* stn 10113 1, 10.ix.1979, 50°16·1′N: 13°31·6′W, 2755–2760 m, 4th ? crab–1 spm 5·1 mm cl., BM(NH) reg. no. 1983: 61. *Discovery* stn 10120 ♯1, 13.ix.1979, 49°27·5′N: 11°21·7′W, 400 m, 4th ? crab–230 spms 5·1–5·5 mm cl., 5th ? crab–25 spms 6·4–6·8 mm cl., 6th ? crab–5 spms 7·1–7·2 mm cl., BM(NH) reg. no. 1983: 15 & 1983: 63.

FOURTH ? CRAB. Carapace (Fig. 2a) broader than long; front less than $\frac{1}{2}$ carapace width, median and submedian lobes developed; orbital dorsal margin forming an even curve, a small incision present. Five prominent, forwardly curved anterio-lateral teeth; 1st, 3rd and 5th acute; 2nd and 4th smaller and subacute.

Pereiopods 2–4 thin; merus of 4th (not figured but see below under *later stages*) margins (and those of carpus) strongly serrate, dactylus styliform, thin and terminally curved, much longer than propodus. Pereiopod 5 (Fig. 5e) merus length about $3\times$ width, dactylus moderately broadened, length slightly less than $4\times$ maximum width and slightly longer than merus + ischium.

LATER STAGES. Specimens assigned here to the 5th and 6th crab stages do not differ significantly from the stage described above, except in having the anterio-lateral spines slightly more pronounced. Pereiopods 2–4 have the same proportions and armature as those attributed to the 4th crab stage. Pereiopod 4 of the 6th ? crab stage is shown in Fig. 5b and for comparison with that of the 6th ? stage of *Bathynectes longipes*; pereiopod 4 is missing from all available earlier stages of this latter species (see below). Pereiopod 4 moderately stout, meral margin serrate, length about $4\times$ width, dactylus much longer than propodus.

(7) *Bathynectes longipes* (Risso)

Post larval stages unknown.

MATERIAL EXAMINED. *Discovery* stn 10110 ♯1, 7.ix.1979, 49°18·8′N: 11°42·8′W, 920–930 m, 5th ? crab–2 spms 5·3–5·6 mm cl., BM(NH) reg. no. 1983: 62. *Discovery* stn 10110 ♯5, 7.ix.1979, 49°17·0′N: 11°50·8′W, 935–1000 m, 5th ? crab–1 spm 5·2 mm cl., 6th ? crab–1 spm 6·9 mm cl., BM(NH) reg. no. 1983: 20. *Discovery* stn 10115♯15, 12.ix.1979, 49°45·4′N: 13°52·9′W, 10–100 m (sounding 3900–4000 m), 4th ? crab–1 spm 4·4 mm cl., BM(NH) reg. no. 1983: 14.

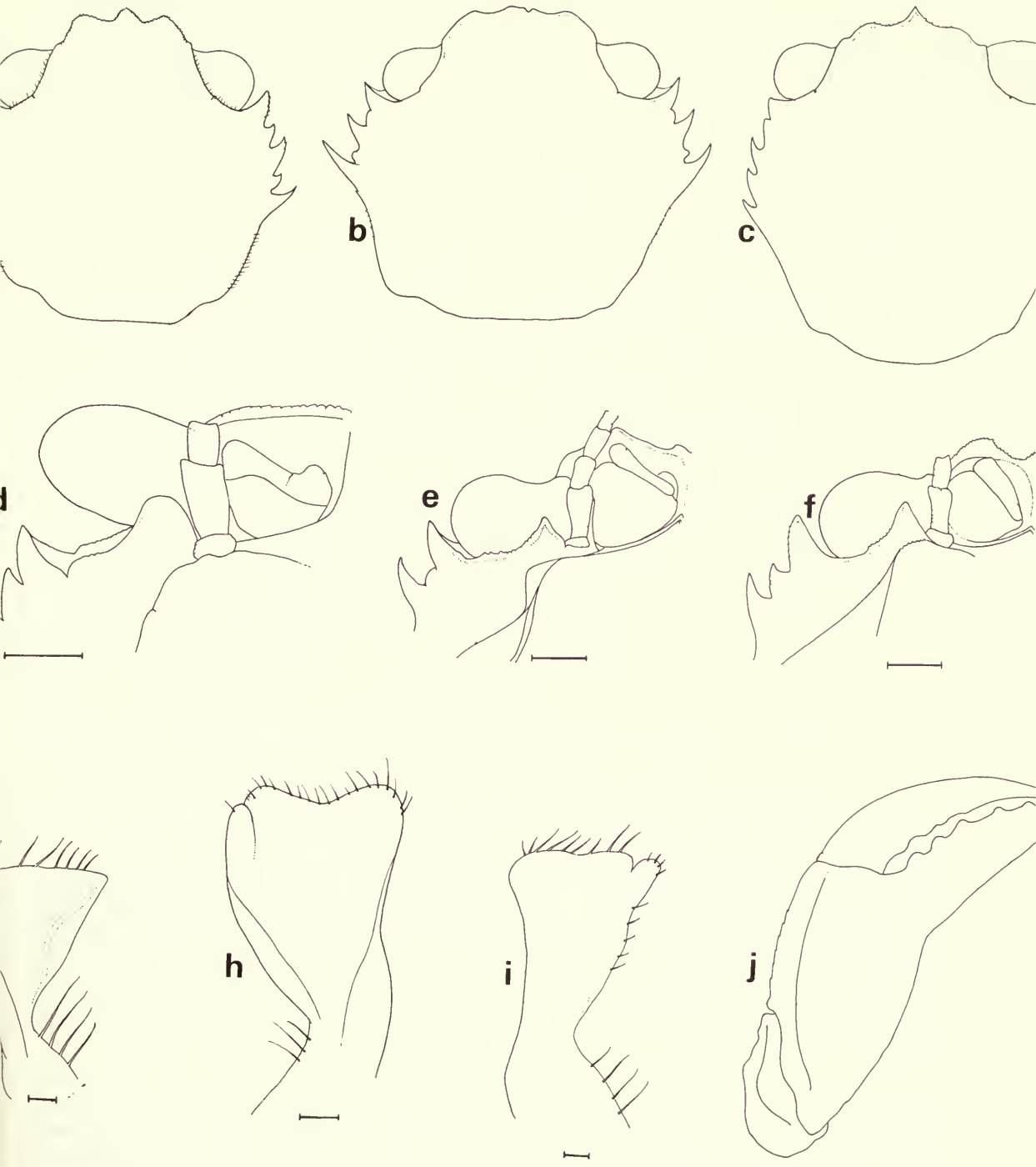

Fig. 2 Outline dorsal aspects of carapace: a, *Macropipus tuberculatus,* 4th ? crab 5·1 mm cl; b, *Bathynectes longipes,* 4th ? crab 4·4 mm cl; c, *Polybius henslowii,* 4th ? crab 4·4 mm cl. Ventral aspect of lower orbital margin: d, *L. puber,* 4th crab; e, *B. longipes,* 4th ? crab; f, *M. tuberculatus,* 5th ? crab (scale = 0·5 mm). Distal part of endopod, 1st maxilliped: g, *P. henslowii,* 4th ? crab; h, *B. longipes,* 4th ? crab; i, *M. tuberculatus,* 5th ? crab (scale = 0·1 mm); j, propodus and dactylus, right cheliped of *P. henslowii,* 4th ? crab (scale = 0·5 mm).

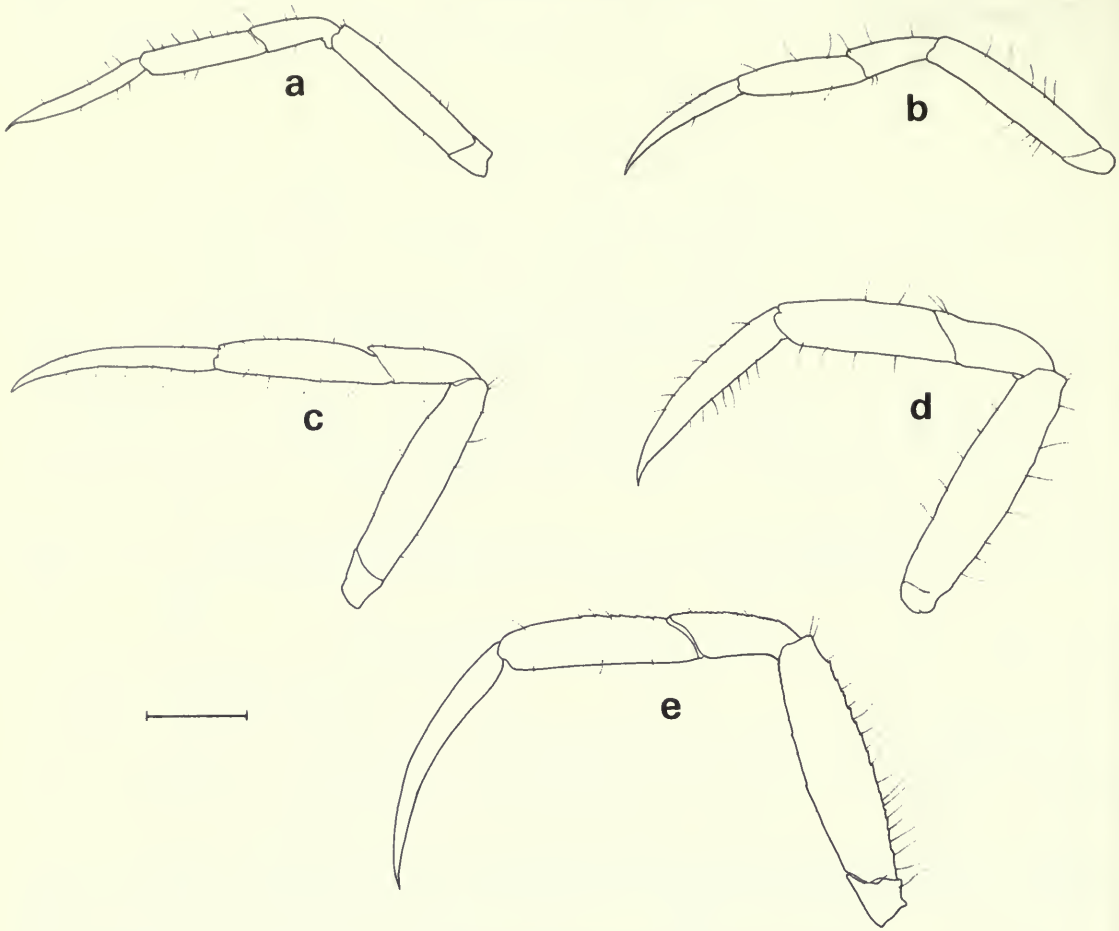

Fig. 3 Outline of 4th left pereiopod, 1st crab: a, *Liocarcinus arcuatus*; b, *L. pusillus*; c, *L. depurator*; d, *L. puber*; e, *L. holsatus* (scale = 0·5 mm).

FOURTH ? CRAB. Carapace (Fig. 2b) broader than long, front less than $\frac{1}{2}$ carapace width, slightly sinuous, lobes not developed, a small median incision; orbital dorsal margin forming a somewhat angular curve and with a small incision. Three prominent, forwardly curved anterio-lateral teeth; 1st, 3rd and 5th acute; 2nd and 4th represented as obtuse lobes; cervical groove moderately defined.

Pereiopods 2–3 thin (4th missing from all specimens of this stage examined, but see below under *later stages*). Pereiopod 5 (Fig. 5f) merus length about $2\frac{3}{4}\times$ width, dactylus moderately broadened, length about $4\times$ maximum width and much longer than merus + ischium.

LATER STAGES. Specimens attributed here to the 5th stage differ only in size from the 4th stage described. The 4th pereiopod of a specimen assigned to the 6th crab stage is shown in Fig. 5c and for comparison with the same stage of *M. tuberculatus* (see Fig. 5b). Pereiopod thin, meral margin serrate, length slightly more than $5\times$ width, dactylus longer than propodus.

(8) ***Polybius henslowii*** Leach

Polybius henslowii, Sivertsen & Holthius 1956: 49, fig. 32f (crab stages).

MATERIAL EXAMINED. *Michael Sars* stn 15, 22–23.iv.1910, 40°56′N: 9°28′W, 50 m, 4th ? crab–2 spms 4·4 & 4·5 mm cl., BM(NH) reg. no. 1983: 58; various stages–18 spms 4·8–10·2 mm cl., Bergen Museum.

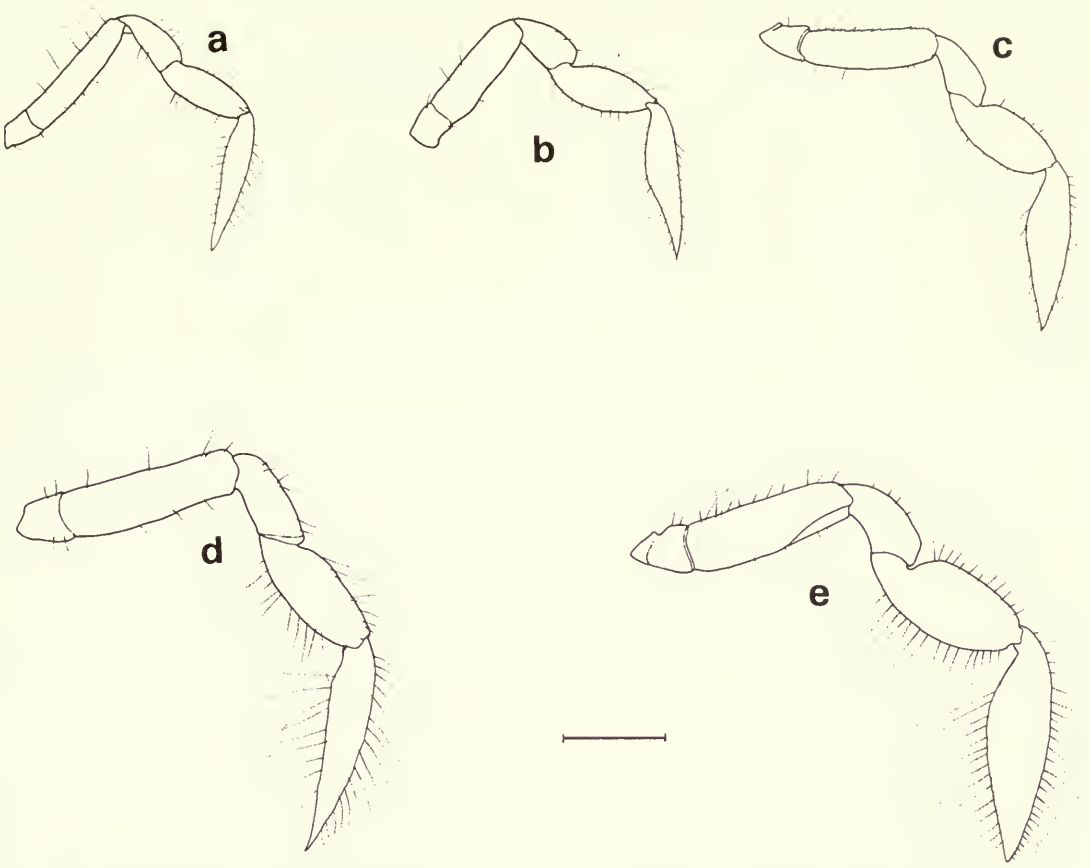

Fig. 4 Outline of 5th left pereiopod, 1st crab: a, *Liocarcinus arcuatus*; b, *L. pusillus*; c, *L. depurator*; d, *L. puber*; e, *L. holsatus* (scale = 0·5 mm).

FOURTH ? CRAB. Carapace (Fig. 2c) slightly longer than broad; front less than $\frac{1}{2}$ carapace width, submedian lobes low and broad, median prominent and acute; orbital dorsal margin forming an even curve and with a small incision. Five prominent, forwardly curved anterio-lateral teeth; 2nd smallest and subacute; 3rd noticeably spinose. All pereiopods of these specimens are detached; the smallest, identifiable as the 4th and that of the 5th figured here, probably belong to the 5th and 6th crab stages respectively.

Pereiopods broad: merus of 4th (Fig. 5a) length slightly more than 3× width, dactylus prominently lanceolate. Pereiopod 5 (Fig. 5d) dactylus broadened, length about $2\frac{1}{4}$× maximum width.

Remarks

Comparative studies of the first crab stages of the five laboratory reared *Liocarcinus* species have revealed two aspects of development. (1) that the species can be arranged in order of overall mean carapace sizes (see Table 1) showing a gradation from the smallest of 1·7 mm (*arcuatus*) to the largest of 2·7 mm (*holsatus*), and (2) that the first crab stage of *holsatus* is morphologically advanced compared with those of the other four species in that the full complement of anterio-lateral teeth are present and similar in shape to those of mature specimens. This definitive adult pattern of carapace teeth is not apparent in *arcuatus, pusillus, depurator* or *puber* until about the third or fourth crab stages (see Lebour 1928: Pl. V, fig. 4, Pl. VI, fig. 1, Pl. VII, figs 1–2).

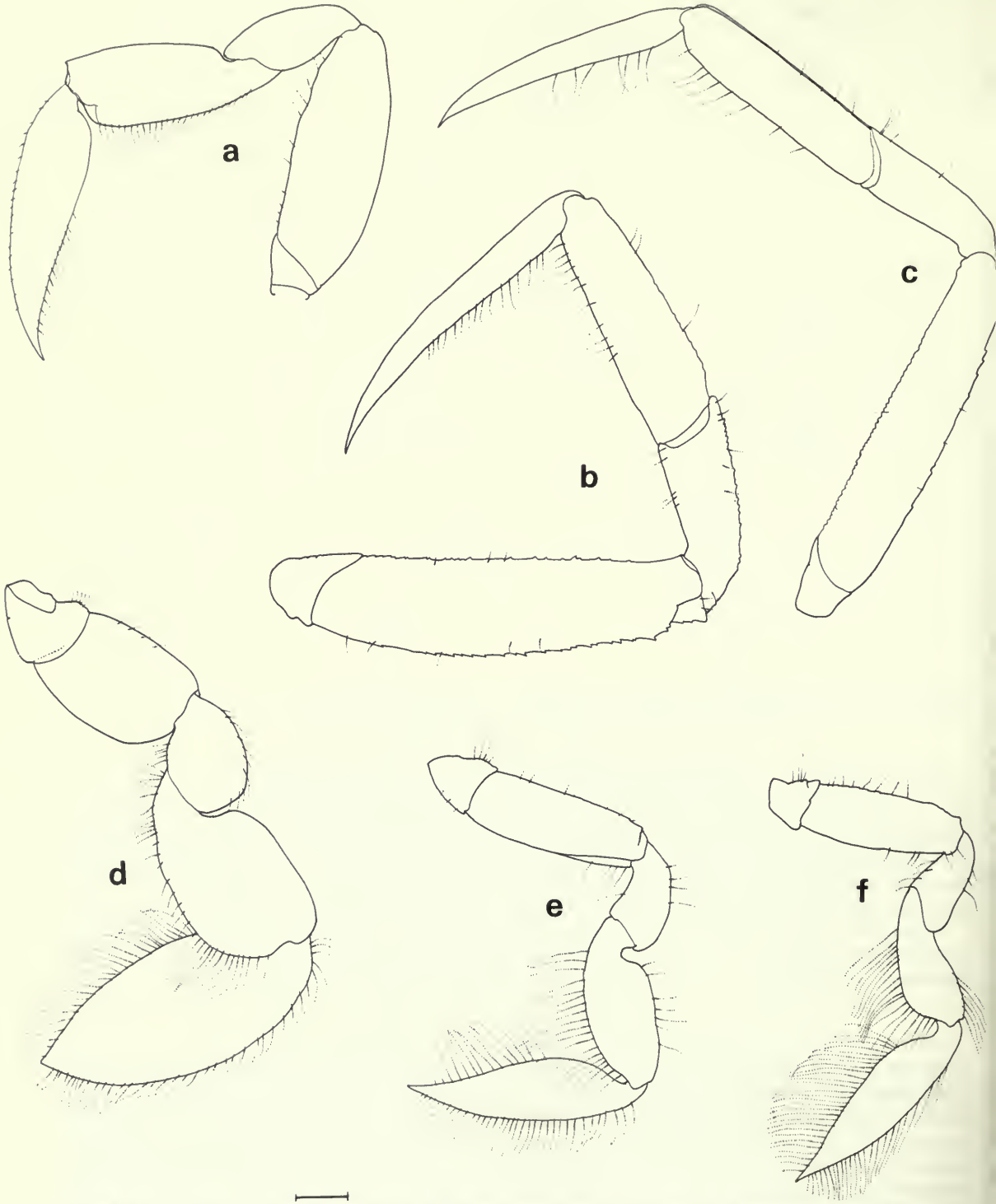

Fig. 5 Outline of 4th left pereiopod: a, *Polybius henslowii,* 5th ? crab; b, *Macropipus tuberculatus,* 6th ? crab; c, *Bathynectes longipes,* 6th ? crab. Outline of 5th pereiopod: d, *P. henslowii,* 6th ? crab; e, *M. tuberculatus*, 5th ? crab; f, *B. longipes,* 5th ? crab (scale = 0·5 mm).

Table 1 Comparative carapace widths of first crab stages of five *Liocarcinus* species. (Mean values are given under PRESENT MATERIAL.)

	LEBOUR (1928)	PRESENT MATERIAL
L. arcuatus	1·6 mm	1·7 mm
L. pusillus	2·0 mm	1·8 mm
L. depurator	3·8 mm	2·2 mm
L. puber	2·8 mm	2·6 mm
L. holsatus	3·2 mm	2·7 mm

Lebour (1928) briefly described the early crab stages of all six species of *Liocarcinus*. The size ranges of her material were similar to those of the laboratory reared specimens of the five species reported here except for *L. depurator* (see below). There are a few apparent differences when our first crab stage material of *arcuatus, pusillus* and *depurator* is compared with Lebour's figures of this stage. The front of *arcuatus* is described by her as 'very slightly three-lobed, hairy', whereas our specimens have a small but distinct median lobe that is strongly deflected ventrally but hardly visible when the carapace is viewed dorsally.

The first crab stage of *L. depurator* figured by Lebour clearly shows all five anterio-lateral teeth well developed; in our material this condition is not reached until the second stage (see Fig. 1e). This feature, and the large carapace size of Lebour's specimen (3·8 mm cw), suggest that her figure is of a second or third crab stage, although the first crab figured by Björck (1913) from plankton caught material measured 3·0 mm. Williamson (1915) figured the first crab stage (presumably obtained from a plankton caught megalopa) that he attributed to *Portunus holsatus*. This figure clearly shows conspicuous, slightly emarginate median and submedian lobes and has a carapace length of about 2·5 mm. These features, and the shape of the anterio-lateral teeth are all characteristic of *depurator* and Williamson's specimen probably belongs to this species. Lebour (1928) also pointed out that the first crab assigned by Williamson to *Portunus puber* is probably an example of *pusillus*; the present study endorses this opinion.

The more advanced crab stages figured here of *Macropipus, Bathynectes* and *Polybius* have carapace lengths approaching those of the 4th–6th crab stages of laboratory reared *L. puber* and *depurator*; they have therefore been tentatively assigned to these respective stages. The carapace shape of juvenile *M. tuberculatus* differs from that of the adult, but it has been possible to identify these early crabs as *Macropipus* because the outer ventral orbital margin is without a v-shaped incision (see Fig. 2f) which is clearly present in *Liocarcinus* juveniles of a corresponding size (see Fig. 2d). This incision is also represented as a shallow notch in juveniles of *Bathynectes longipes* (see Fig. 2e).

The juveniles of *B. longipes* have been identified on the following combined features. (1) the narrow second segment of the antennal peduncle which does not fill the gap between the lower inner orbital margin and the frontal region; (2) the long slender pereiopods (Fig. 5c); (3) the noticeable alternation in size of the anterio-lateral teeth; (4) the undeveloped submedian and shallow median lobes of the front; (5) the moderately defined cervical groove. All these features are found in the adult *B. longipes*.

The carapace shape of juvenile crabs attributed to *Polybius henslowii* also differ from the adult form but these juveniles can be readily identified by the lanceolate dactyls of the 2nd–4th pereiopods (Fig. 5a) and the distinctive shape of the cheliped (Fig. 2j); both are features of the adult crab. However, the juveniles of 4·4 mm cl. (4th ? crab) are without a lobe on the first maxilliped endopod (see Fig. 2g) which is prominent in adults of *P. henslowii* and is also developed in juveniles of a similar size of *M. tuberculatus* (see Fig. 2i), *Bathynectes longipes* (see Fig. 2h) and in corresponding stages of the *Liocarcinus* species examined.

Acknowledgements

We wish to express our thanks to Dr David McGrath, University College, Galway, for assisting with the collecting of ovigerous *Liocarcinus arcuatus*. We also thank Endre Willassen, University of Bergen, for donating two specimens of *Polybius henslowii* from the *Michael Sars* North Atlantic Deep-Sea Expedition (1910) to the Collections of the British Museum (Natural History).

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The freeliving marine nematode genus *Sabatieria* (Nematoda: Comesomatidae). II. Redescriptions of five European species

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Introduction

This is the second in a series of papers examining in detail several species of *Sabatieria* in preparation for a general review of the genus. It contains further data on *S. celtica* Southern, 1914 (including new specimens from the type locality), *S. breviseta* Stekhoven, 1935, *S. punctata* (Kreis, 1924), *S. longispinosa* Lorenzen, 1972 and *S. elongata* Jayasree & Warwick, 1977. All species are fully illustrated with line drawings and photographs. Methods and abbreviations are as given in Platt (1982, 1983).

Systematic descriptions

Sabatieria celtica Southern, 1914
Figs 1–5

MATERIAL STUDIED. 1♀ from Clew Bay, Co. Mayo, Ireland BM(NH) 1915.1.1.15, labelled '♀ co-type', collected by Southern (1914) from sand and shells at 40 m. 2♂♂, 2♀♀ and 2 juveniles from Clew Bay, BM(NH) 1982.7.82–84, collected July 1980 from shelly gravel at 17 m, about 0·5 km east of harbour on Clare Island. 5♂♂ and 1♀ from Strangford Lough, Northern Ireland, BM(NH) 1981.12.124, 1982.7.85–88, high tide station (see Platt, 1977). Several males and females from Cullercoats, Northumberland coast, England, BM(NH) 1980.5.62, collected by Dr R. M. Warwick.

MEASUREMENTS (in μm), DEMANIAN RATIOS AND MERISTIC DATA
Males (♂1–♂5 from Strangford Lough and ♂6–♂7 from Clew Bay respectively). Total body length: 2135; 1800; 2030; 1770; 2085; 2940; 2560. Demanian ratio a: 39; 38; 41; 31; 37; 43; 44. Demanian ratio b: 9·2; 7·5; 9·0; 7·4; 7·8; 10·2; 9·4. Demanian ratio c: 14·4; 12·8; 13·2; 12·4; 14·5; 14·3; 13·0. R3 sensilla length: 9; 10; 9·5; 8; 8; 19; –. Head diameter: 16; 16; 17; 18; 17; 20; 20. Amphid diameter: 12; 11; –; 11; 11; 14; –. Amphid c.d.: 19; 17; 21; 19; 19; 22; –. Oesophagus length: 233; 241; 226; 241; 268; 287; 273. Maximum body diameter: 55; 48; 50; 57; 56; 69; 58. Spicule length (chord): 46; 47; 51; 55; 50; 60; 56. Anal body diameter: 45; 37; 42; 44; 59; 50; 47. Number of precloacal supplements: 21; 16; 16; 19; –; 20; 21. Cloaca to anterior supplement (β): 255; 202; 238; 262; –; 215; 228. Tail length: 148; 141; 154; 143; 144; 205; 197.

DESCRIPTION. This species has been redescribed by Lorenzen (1972): the following information is based on recent specimens from Ireland.

Cuticle has lateral differentiation of larger and less closely spaced dots (Fig. 4). In the oesophagus and tail region, the lateral dots are irregularly arranged but in the mid-body region they appear to be arranged in transverse rows. Short sublateral somatic setae present throughout the body. Cervical somatic setae are slightly larger than the general somatic setae, especially in the Clew Bay specimens. The first, anteriormost cervical seta always appears to be situated ventro-sublaterally. R3 sensilla 45–62% c.d. in Strangford Lough specimens, 80–95% c.d. in Clew Bay specimens. Amphids describe 2½ turns, 58–69% c.d. wide (males). Excretory pore at 62–66% of oesophagus length: lateral supplementary cells not detected in the males. Tail conico-cylindrical, 3·1–4·1 a.b.d.: conical part about 50% of total.

Bull. Br. Mus. nat. Hist. (Zool.) **46**(4): 355–375 Issued 31 May 1984

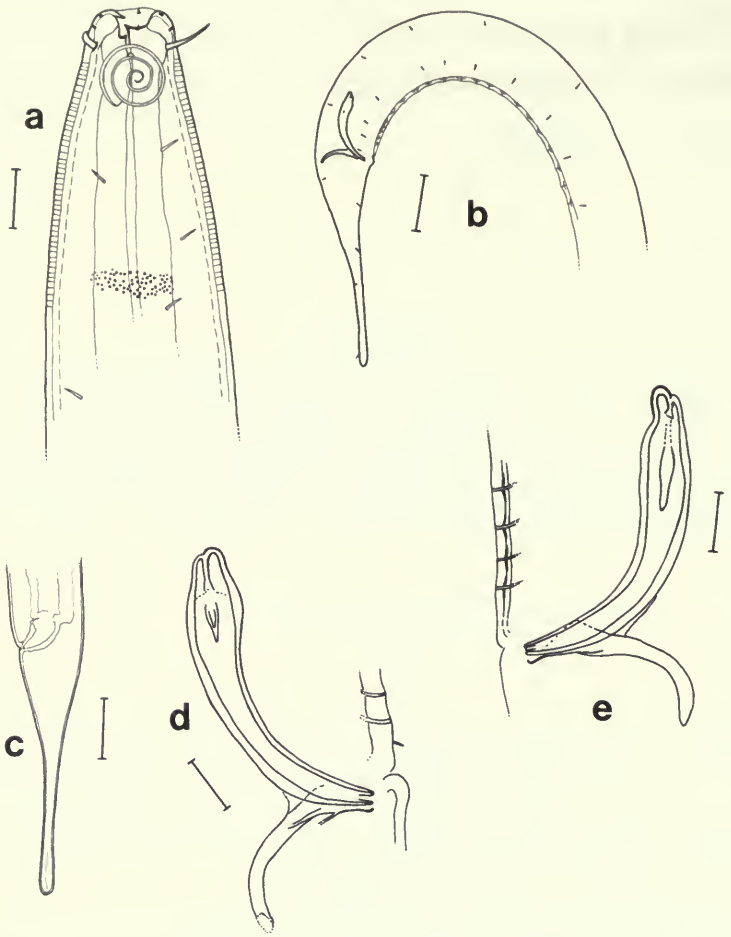

Fig. 1 *Sabatieria celtica* from Strangford Lough: (a) ♂1 head; (b) ♂1 posterior region; (c) ♀1 tail; (d) ♂3 copulatory apparatus; (e) ♂5 copulatory apparatus. Bar scales: b, c = 40 μm; others = 10 μm.

Spicules equal, curved: 1·2–1·3 a.b.d. as chord. Gubernaculum apophysis distinctly curved, about half the length of the spicule, but often the exact proximal extremity is difficult to distinguish. Short precloacal spine and 16–21 tubular supplements, occupying 11·2–14·8% of total body length in Strangford specimens but only 7·3 and 8·9% in those from Clew Bay. Two opposed testes: anterior left, posterior right of gut.

Ovaries opposed, outstretched: anterior left, posterior right of gut.

Remarks. The specimens described here, including those from the type locality, are identical with those described by Lorenzen (1972) from sublittoral sediment near Helgoland. The only surviving representative of Southern's (1914) original type material is the co-type female, but this is in poor condition and almost completely flattened. However, what characters that are visible, such as the amphid, cuticle pattern (Fig. 4g–h) and tail shape agree with the new material. Southern apparently overlooked the precloacal supplements in his male, but this is easily done if the worm is not viewed exactly from a lateral aspect. The only remaining difference between Southern's description and the specimens described here and by Lorenzen is the shape of the distal tip of the spicules—Southern shows them as being distinctly wedge-shaped (Fig. 2c). It must be concluded that Southern's specimen was anomalous in

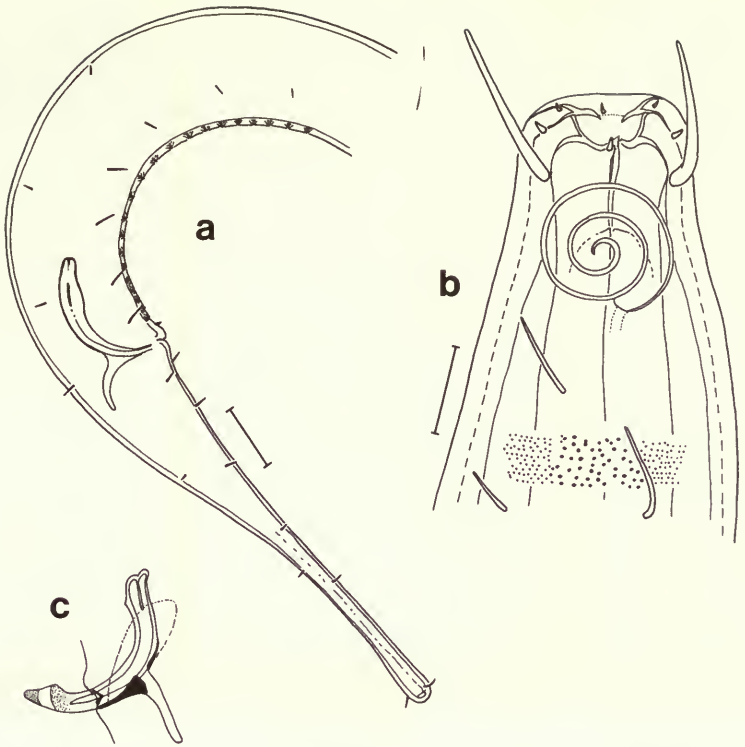

Fig. 2 *Sabatieria celtica* from Clew Bay: (a) ♂7 posterior region; (b) ♂6 head; (c) spicule of Southern's male (after Southern, 1914). Bar scales: a = 30 μm; b = 10 μm.

this respect. Interestingly enough, several other species described by Southern (1914) from Clew Bay were also represented in my material, tending to support the *Sabatieria* specimens as being conspecific.

The material from Helgoland described by Lorenzen (1972) showed a wide range in the intraspecific variation of certain characters, especially the relative R3 sensilla length (64–124% c.d.). As observed by Jensen (1979), this is unusual for *Sabatieria* species, particularly in specimens from the same locality. The Irish material also showed variation in this character, from 45–95% c.d. overall, although the within-habitat variation does not appear to be as great as Lorenzen reported for his material. Nevertheless, it underlines the dangers of relying too heavily on morphometric data rather than meristic or detailed anatomical characters.

Pearse, Humm & Wharton (1942) recorded *S. celtica* from intertidal sand at Beaufort, North Carolina, U.S.A. However, a detailed investigation of material collected in August 1980 from the same locality failed to reveal any *Sabatieria* specimens resembling *S. celtica,* although two other *Sabatieria* species were encountered, as will be described elsewhere.

Sabatieria breviseta Stekhoven, 1935
Figs 6–11

MATERIAL STUDIED. 3♂♂ and 2♀♀ on slides BM(NH) 1982.7.69–70. Found in dead *Diastylis rathkei* (Krøyer) (Crustacea: Cumacea) taken from Swansea Bay, May 1975, collected by Dr R. M. Warwick.

MEASUREMENTS (in μm) AND DEMANIAN RATIOS
Males (♂1–♂3 respectively). Total body length: 1160; 1105; 1220. Demanian ratio a: 33; 37; 39. Demanian ratio b: 8·1; 7·9; 8·1. Demanian ratio c: 11·1; 11·9; 11·6. R3 sensilla length: 4; 4; 3. Head

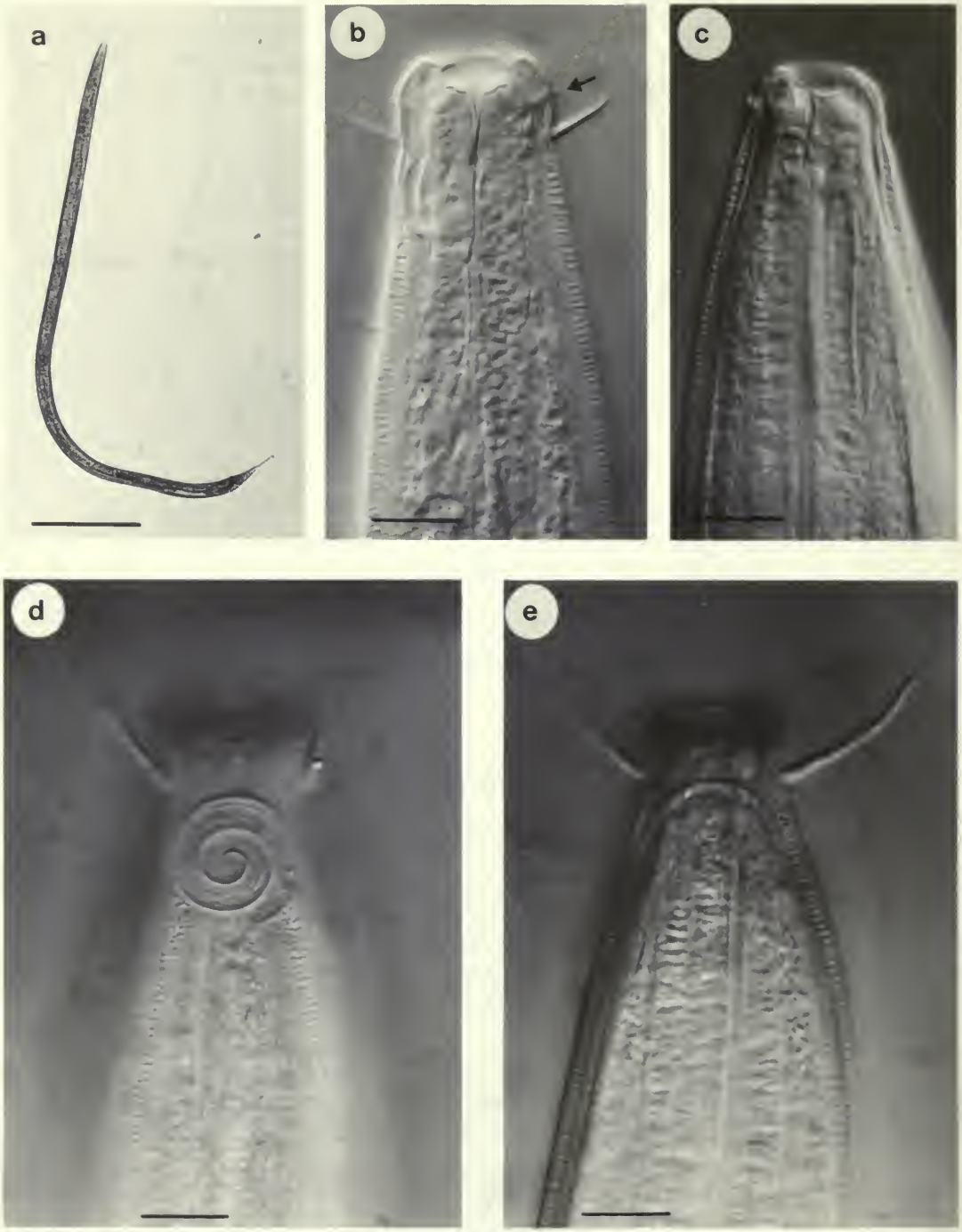

Fig. 3 *Sabatieria celtica* from Strangford Lough (a–c) and Clew Bay (d–e): (a) entire ♂; (b) head showing R2 (arrow) and R3 sensilla; (c) head showing buccal dentition; (d) head showing amphid; (e) head showing R3 sensilla. Bar scales: a = 300 µm; others = 10 µm.

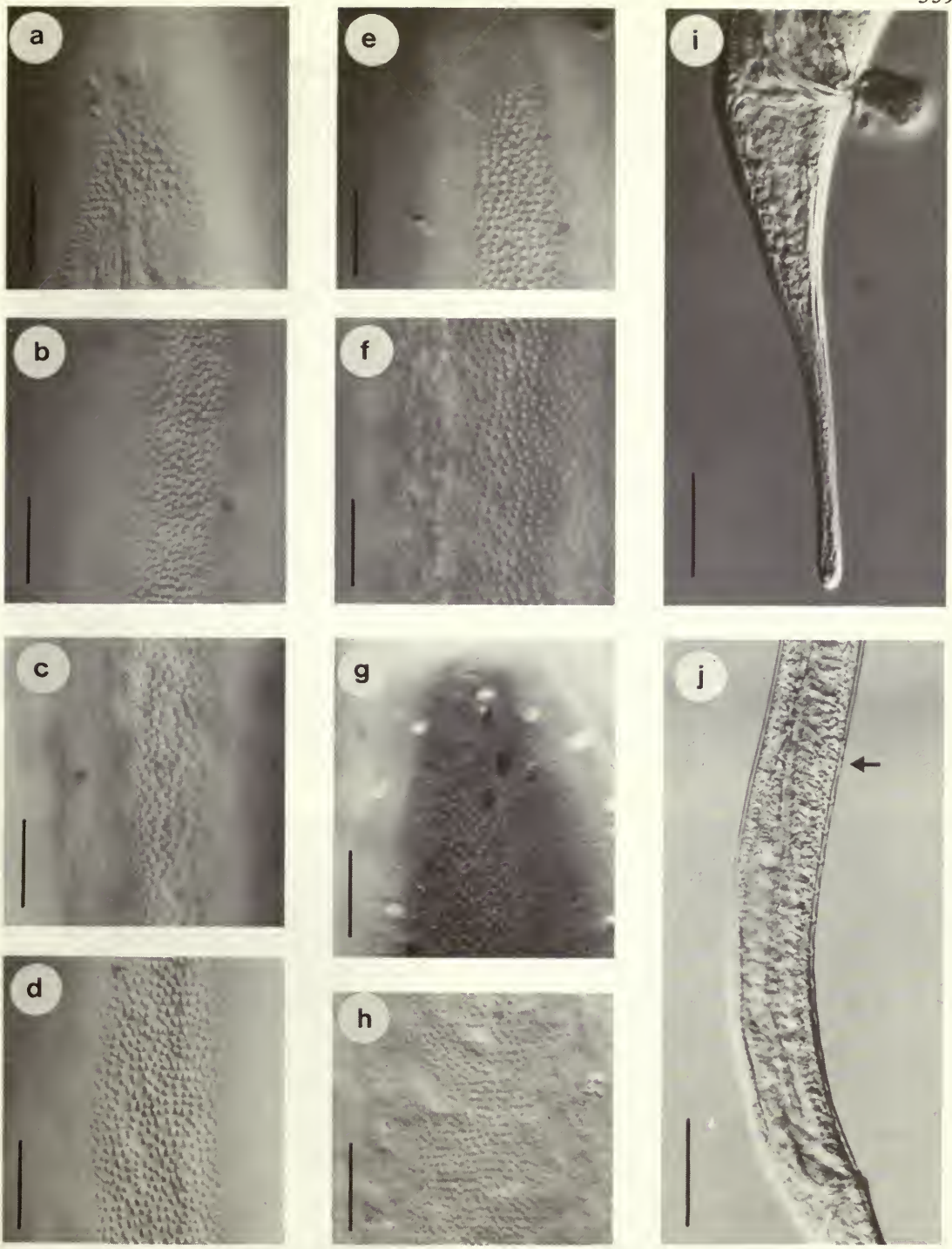

Fig. 4 *Sabatieria celtica* from Strangford Lough (a–d and i–j) and Clew Bay (e–h): (a) cuticle immediately post-amphid; (b) cuticle mid-body; (c) cuticle mid-body but showing sub-lateral pattern; (d) cuticle in cloacal region; (e) cuticle immediately post-amphid; (f) cuticle mid-body; (g) cuticle of Southern's cotype ♀ immediately post-amphid; (h) cuticle of Southern's cotype ♀ mid-body; (i) ♂ tail; (j) anterior cloacal region showing supplements, anteriormost arrowed. Bar scales: i = 30 μm; j = 50 μm; others = 10 μm.

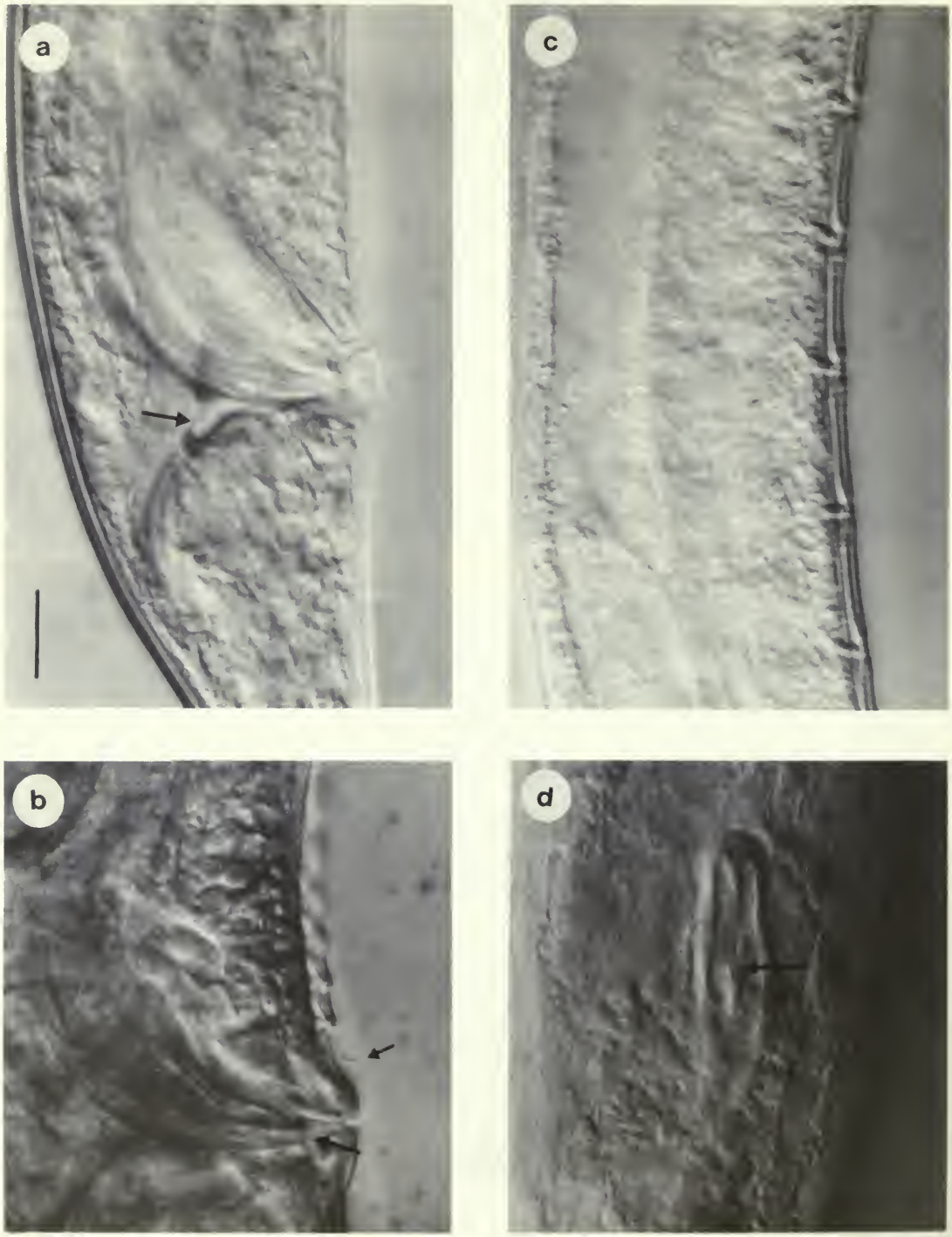

Fig. 5 *Sabatieria celtica* from Strangford Lough: (a) cloacal region showing median piece of gubernaculum (arrow); (b) cloacal region showing precloacal spine (small arrow) and spicule tip (large arrow); (c) detail of anterior precloacal supplements; (d) proximal end of spicule showing median list (arrow). Bar scales: for all, as in a = 10 μm.

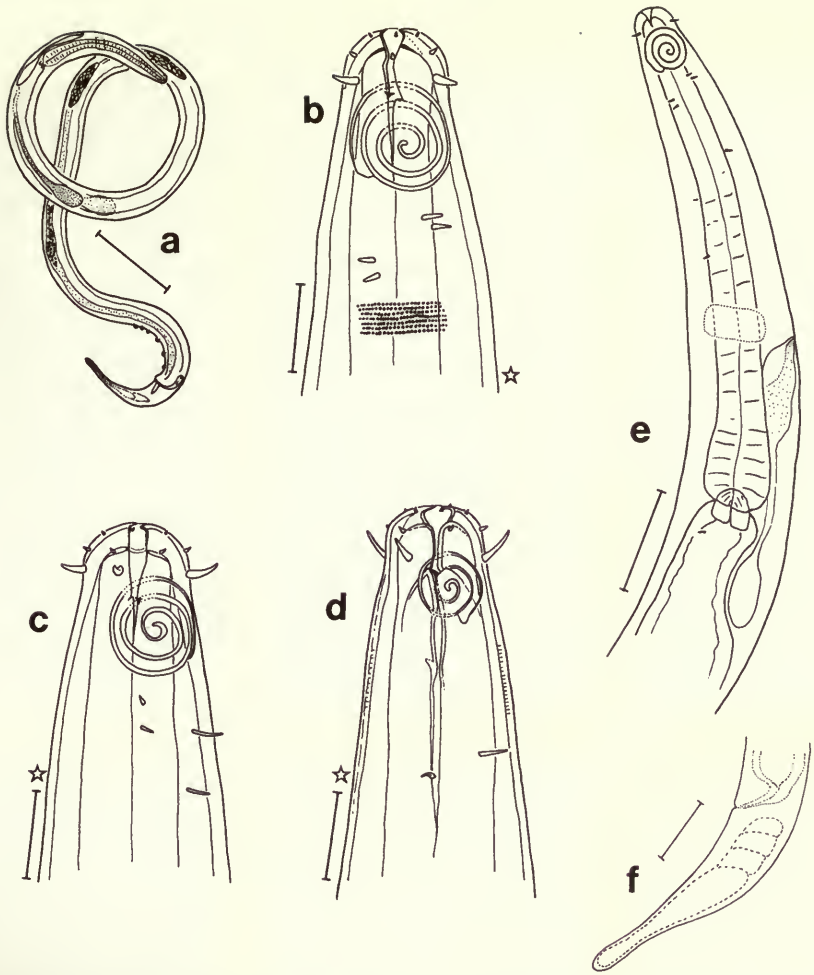

Fig. 6 *Sabatieria breviseta* from Swansea Bay: (a) ♂3 entire body; (b) ♂1 head; (c) ♂2 head; (d) ♀1 head; (e) ♂1 anterior region; (f) ♀2 tail. Stars indicate ventral side. Amphids in b, c and d shown in part with hatched lines to avoid obscuring buccal cavity details. Bar scales: a = 100 μm; e, f = 30 μm; others = 10 μm.

diameter: 12; 12; 12. Amphid diameter: 12; 11·5; –. Amphid c.d.: 14; 14·5; –. Oesophagus length: 144; 140; 150. Posterior oesophagus c.d.: 32; 29; 31. Maximum body diameter: 35; 30; 31. Spicule length (chord): 34; 34; 33. Anal body diameter: 28; 26; 27. Cloaca to anterior supplement (α): 74; 89; 74. Cloaca to anterior supplement (β): 106; 108; 113. Tail length: 105; 93; 105.

Females (♀1–♀2 respectively). Total body length: 1195; 1340. Demanian ratio a: 36; 38. Demanian ratio b: 8·1; 8·6. Demanian ratio c: 12·0; 13·1. R3 sensilla length: 4·5; 4·5. Head diameter: 11; 11. Amphid diameter: 7·5; 7·5. Amphid c.d.: 12·5; 13. Oesophagus length: 148; 156. Posterior oesophagus c.d.: 32; 33. Maximum body diameter: 33; 35. Anal body diameter: 25; 28. Tail length: 100; 102. Vulva to anterior: 595; 687. Vulva c.d.: 35; 37.

DESCRIPTION. Posterior half of mid-body region generally about 10% narrower than the anterior part: the diameter anterior to the mid-point has been used to calculate the 'a' ratio. Cuticle punctated: fine lateral dots in transverse rows, slightly larger and more visible than the sublateral ones, especially in oesophagus and tail regions. Dots in the mid-body region often beyond resolution. 20 rows per 10 μm in lateral field throughout body. Short scattered 2–3 μm sublateral somatic setae throughout body. In males, there is a ventro-sublateral pair

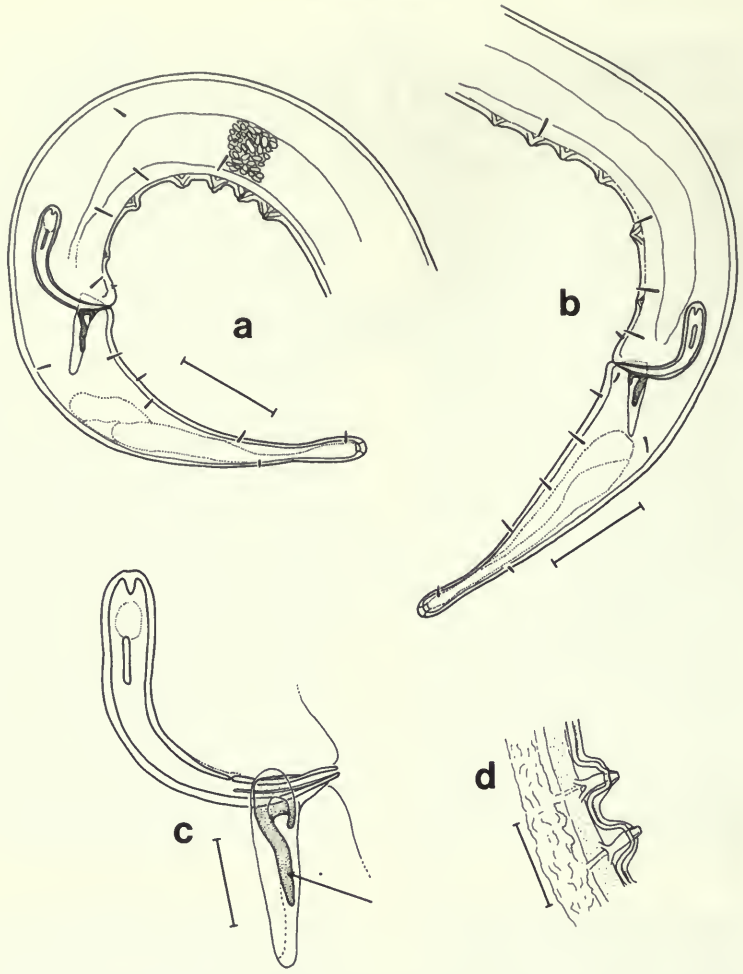

Fig. 7 *Sabatieria breviseta* from Swansea Bay: (a) ♂1 posterior region; (b) ♂2 posterior region; (c) ♂1 copulatory apparatus, median piece arrowed; (d) detail of two of ♂3 precloacal supplements. Bar scales: a, b = 30 μm; c, d = 10 μm.

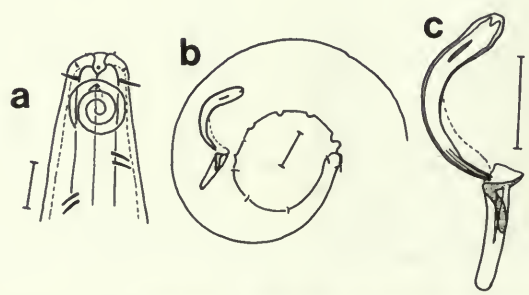

Fig. 8 *Sabatieria breviseta* from Helgoland, from an unpublished drawing by Dr P. Jensen from Lorenzen's (1974) Helgoland material (slide A62/4): ♂ head; (b) ♂ posterior region; (c) copulatory apparatus. Bar scales: a = 10 μm; b, c = 20 μm.

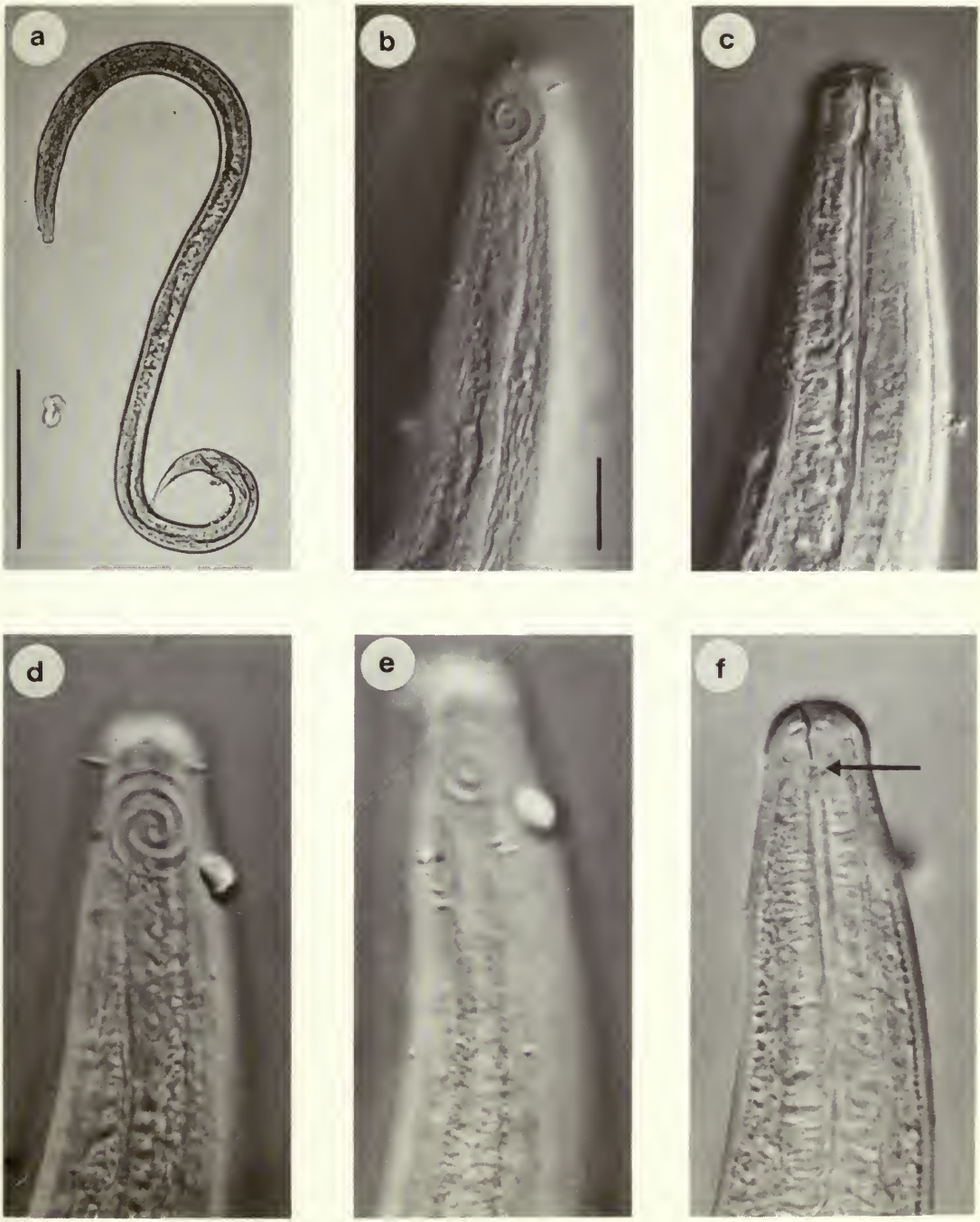

Fig. 9 *Sabatieria breviseta* from Swansea Bay: (a) entire ♂; (b) ♀ amphid; (c) ♀ buccal cavity; (d) ♂ amphid; (e) ♂ cervical setae, also note cuticle pattern; (f) ♂ buccal cavity showing tooth (arrow). Bar scales: a = 200 μm; for others, as in b = 10 μm.

Fig. 10 *Sabatieria breviseta* from Swansea Bay: (a) cuticle post-amphid; (b) cuticle mid-body, difficult to distinguish but frequency of the transverse rows of lateral dots shown by the bars; (c) ♂ anterior region showing excretory ampulla (a), end of oesophagus (o) and position of supplementary cell (s); (d) posterior oesophagus region showing excretory ampulla (arrow); (e) detail of supplementary excretory cell. Bar scales: c = 50 μm; others = 10 μm.

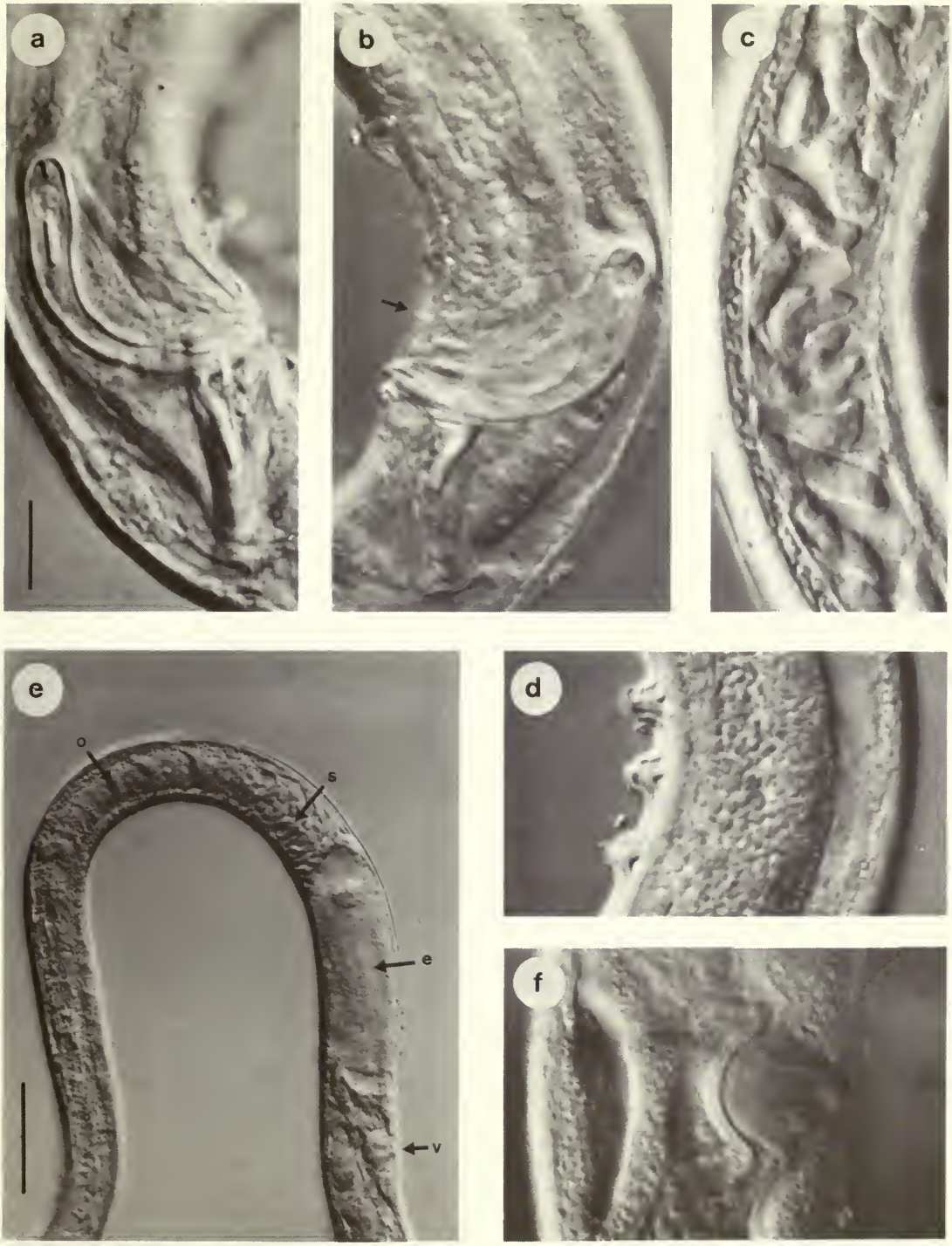

Fig. 11 *Sabatieria breviseta* from Swansea Bay: (a) copulatory apparatus; (b) copulatory apparatus of another specimen showing slightly different appearance of gubernaculum median piece, precloacal spine (arrow) and first two supplements; (c) sperm in ♂; (d) detail of three anterior supplements; (e) mid-body region of ♀ showing outstretched ovary (o), spermatheca with sperm (s), elongated egg (e) and vulva (v); (f) detail of vulva region. Bar scales: e = 50 μm; for others, as in a = 10 μm.

of cervical setae just posterior to amphid and a dorso-sublateral pair slightly posterior to them (Figs 6b, c and 9e): absent in females (Fig. 6d). R1 and R2 sensilla conical but conspicuous. R3 sensilla 3–4 μm in males (30% h.d.), 4·5 μm in females (40% h.d.). Amphids describe 3½ turns in males, but only 3 turns in females: about 80–85% and 60% c.d. respectively. Anterior part of buccal cavity small and expanded and generally cup-shaped, but in certain specimens it can appear almost conical (Fig. 6b). Posterior tubular section has a conspicuous dorsal projection (tooth?) at its base (Fig. 9f). Oesophagus has an expanded posterior part. Nerve ring at about 60% of oesophagus length. Excretory pore at 64–70% of oesophagus length with a conspicuous ampulla (Fig. 10d). Ventral gland conspicuous. In males, there are also two large lateral supplementary cells situated just over two oesophagus lengths from the anterior with ducts leading anteriorly (Figs 10c, e), but their termination could not be detected: these supplementary cells may not always be easily detectable. Tail 3·6–4·0 a.b.d., conico-cylindrical: conical part about 70% of total but an actual cylindrical part is almost non-existent before the swollen tip. Caudal glands conspicuous and lying entirely in the tail.

Spicules equal, curved: 1·2–1·3 a.b.d. as chord; 1·5–1·6 a.b.d. (40–44 μm) as arc. Gubernaculum surrounds distal ends of spicules and has paired dorso-caudally directed apophyses, each about 18 μm long (about 53% of spicule chord length) and with a prominent cuticularised median piece (Figs 11a, b): gubernaculum median piece is less distinct when not viewed from a lateral aspect. Ventral spine situated about 7–8 μm precloacally. Six prominent precloacal supplements, the first 14–17 μm (α) from the cloaca and not as conical as the others: anteriormost three (sometimes four) closer together than the others. Anterior supplement situated 106–113 μm (β) from cloaca; 9·1–9·8% of total body length. Each supplement has a duct leading to an elongated subcuticular amorphous gland lying between the body wall and the vas deferens: distinct glands associated with each supplement could not be detected. Two opposed testes: anterior left, posterior right of gut.

Ovaries opposed, outstretched: anterior left, posterior right of gut. Vulva conspicuous; V = 50–51%. Vagina conspicuous, well cuticularised and with distal glands (Fig. 11f). Eggs elongated, about 35 × 100 μm (Fig. 11e). Receptaculum seminis of mature females contain small oval sperm (Fig. 11e).

Remarks. The original description of this species was given by De Coninck & Stekhoven (1933) based on a single female specimen from Belgium, although at first they believed it to be *S. quadripapillata* Filipjev, 1922. However, this opinion was later revised on finding a male and three more females, also from Belgium, which clearly differed from Filipjev's description, and Stekhoven (1935) gave the specimens a new name—*S. breviseta.* Stekhoven (1936, 1942) recorded the species twice more from the North Sea. Based on material from a sublittoral area near Helgoland, Lorenzen (1974) eventually synonymised *S. breviseta* with *S. pulchra* (G. Schneider, 1906), in the belief that he had found transition states between the two species in terms of R3 sensilla length, amphid size and precloacal supplement characters. However, Jensen (1981) concluded that Lorenzen's material did in fact contain distinct specimens referrable to *S. breviseta.* Figure 8 is Dr Jensen's drawing of Lorenzen's (1974) *S. breviseta,* clearly showing the large 3½-turn amphid (as described by Stekhoven) and the large median piece of the gubernaculum, characters which differentiate the species from *S. pulchra.*

Sabatieria punctata (Kreis, 1924)
Figs 12–13

Material studied. ♂1, ♂2 and ♀1 from Swansea Bay on slides BM(NH) 1981.12.125, 1982.7.69; 2♂♂ from Northumberland on slide BM(NH) 1980.5.3. Swansea Bay: specimens taken from dead *Diastylis rathkei* (Krøyer) (Crustacea: Cumacea), collected by Dr R. M. Warwick, May 1975. Northumberland: 2 miles east of Lynemouth, very fine sand at 35 m depth (Station A; Warwick & Buchanan, 1970).

Measurements (in μm) and demanian ratios
♂1, ♂2 and ♀1 respectively. Total body length: 1160; 1095; 1160. Demanian ratio a: 36; 33; 28. Demanian ratio b: 8·5; 7·8; 7·9. Demanian ratio c: 11·1; 11·9; 10·6. R3 sensilla length: 4; 4; 4. Head diameter:

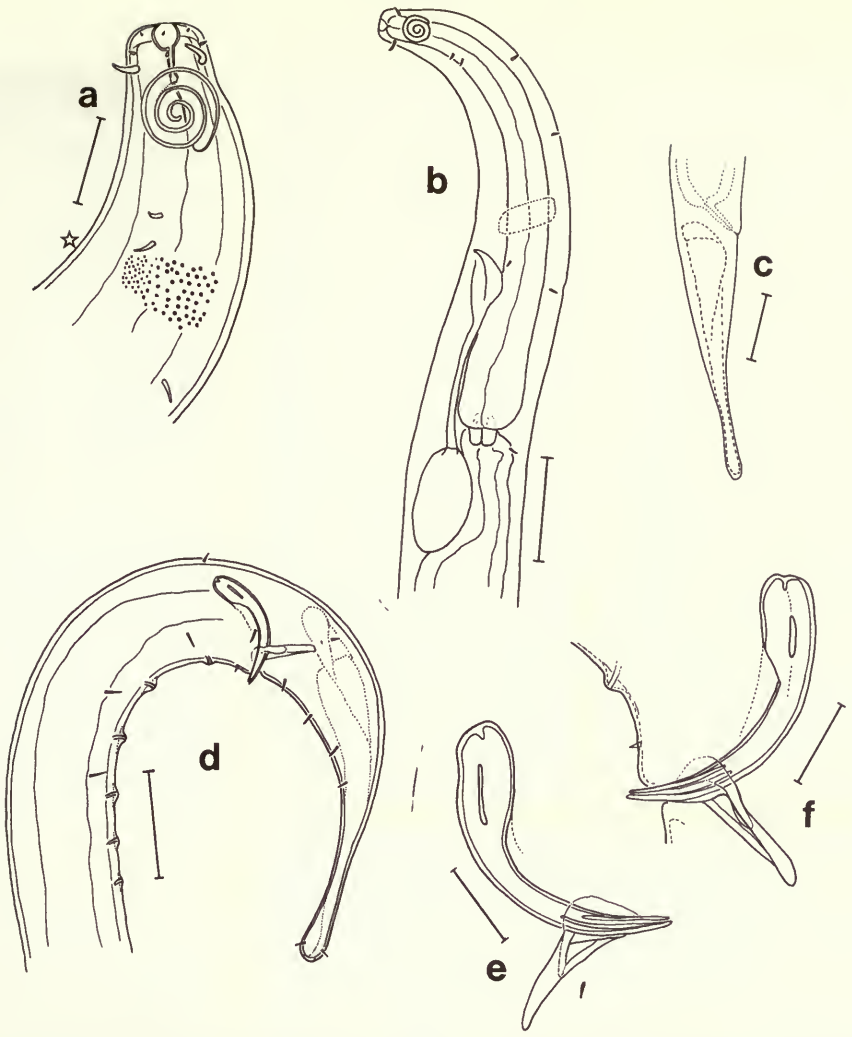

Fig. 12 *Sabatieria punctata* from Swansea Bay: (a) ♂1 head, star indicates ventral side; (b) ♂1 anterior region; (c) ♀ tail; (d) ♂1 posterior region; (e) ♂2 copulatory apparatus; (f) ♂1 copulatory apparatus. Bar scales: b, c, d = 30 μm; a, e, f = 10 μm.

9·5; 10·5; 10·5. Amphid diameter: 8·5; –; –. Amphid c.d.: 12; –; –. Oesophagus length: 136; 141; 147. Posterior oesophagus c.d.: 32; 30; 36. Maximum body diameter: 32; 33; 41. Anal body diameter: 28; 29; 28. Tail length: 105; 92; 110. Spicule length (chord): 31; 32. Cloaca to anterior supplement (α): 88; 114. Cloaca to anterior supplement (β): 117; 113.

DESCRIPTION. Posterior half of mid-body region only slightly narrower than anterior part. Cuticle punctated: lateral differentiation of larger dots in fewer rows. The lateral differentiation is most conspicuous in the oesophagus and the conical part of the tail, where some of the dots appear to be elongated (Fig. 13e): although the dots are rather irregularly arranged in the lateral field, just posterior to the amphid there are about 11 rows per 10 μm and on the tail 8 rows per 10 μm. The lateral dots in the mid-body region are smaller than those at the extremities but irregularly arranged (Fig. 13d). Just ventral to the lateral field, there are about 17–20 rows of dots per 10 μm. In males from Swansea Bay, there is a pair of ventro-sublateral cervical setae and a single dorso-sublateral seta situated further posterior (Fig. 12a): in the Northumberland males, however, there is a pair of setae situated dorso-

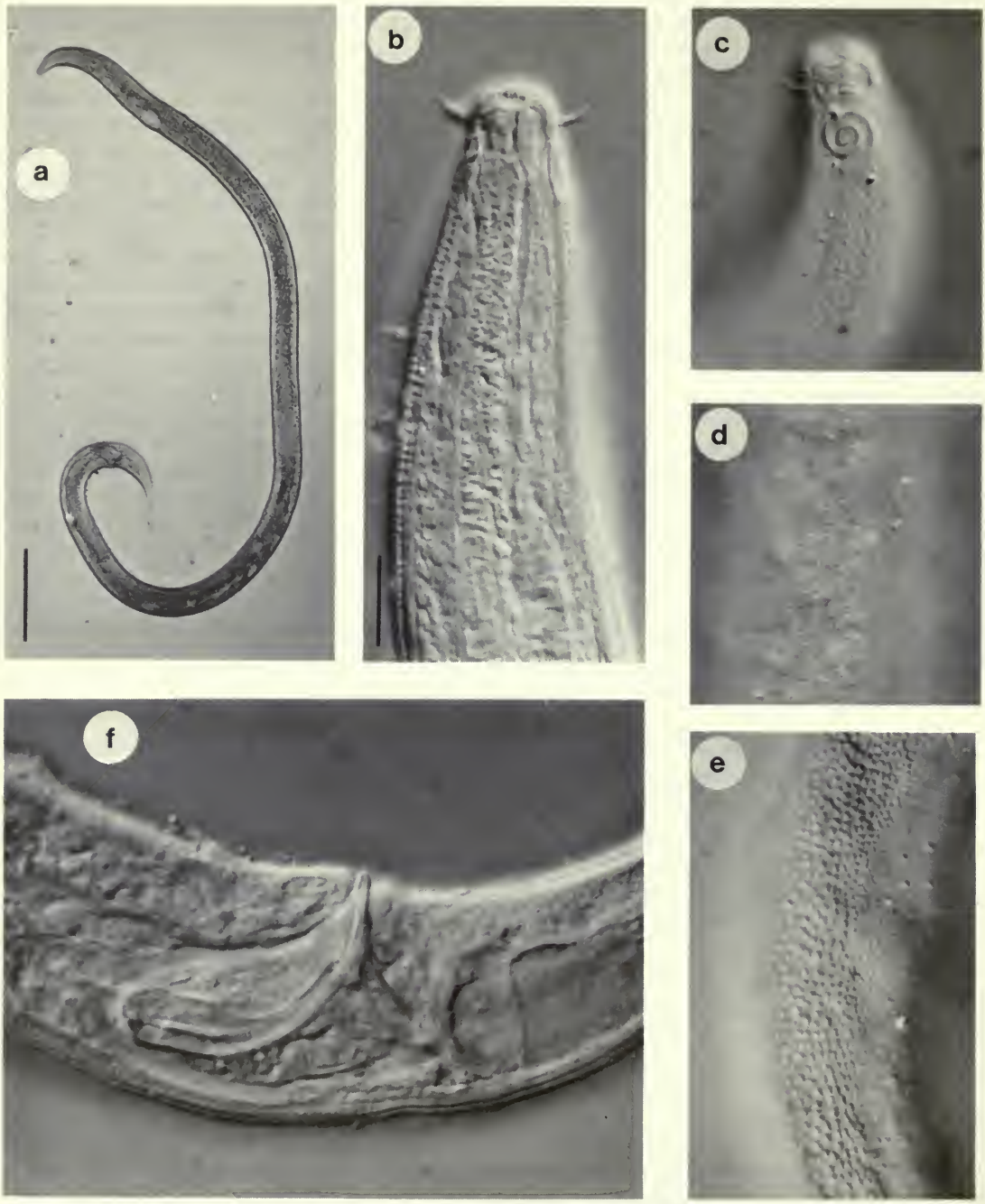

Fig. 13 *Sabatieria punctata* from Swansea Bay: (a) entire ♂; (b) anterior region showing R3 sensilla; (c) anterior region showing amphid and lateral cuticle pattern; (d) lateral cuticle mid-body; (e) lateral cuticle in cloacal region; (f) copulatory apparatus. Bar scales: a = 100 μm; for others, as in b = 10 μm.

sublaterally, as in *S. breviseta*. R1 and R2 sensilla conical. R3 sensilla 38–42% h.d. in both sexes. Amphids describe 3 turns: 70% c.d. wide in ♂1 (♂2 and ♀ amphids obscured). Nerve ring and excretory pore at about 50–55% and 60–65% of oesophagus length respectively. In males, supplementary lateral excretory cells present. Tail 3·2–3·9 a.b.d., conico-cylindrical : conical part about 70% of total with a short cylindrical section before the swollen tip.

Spicules equal, curved: 1·1 a.b.d. as chord; 1·3 a.b.d. as arc. Gubernaculum apophysis 12–14 μm long (about 40–45% of spicule chord length): a conspicuous median piece could not be detected. Ventral spine and six precloacal supplements: anterior supplement situated 105 μm (♂1) and 92 μm (♂2) from cloaca (β), 10·1 and 10·3% of total body length respectively. Two opposed testes: anterior left, posterior right of gut.

Ovaries opposed, outstretched: anterior right, posterior left of gut: V = 51%.

REMARKS. In almost all respects, the specimens appear identical to those described from the Øresund by Jensen (1979). There is some variation in the number of sublateral rows of punctations (per 10 μm) but the general pattern is similar.

S. punctata was until recently considered synonymous with *S. pulchra* (G. Schneider, 1906): indeed, Kreis's original (1924) description was such that it could fit almost any *Sabatieria* species with about six precloacal supplements. However, Jensen's (1979) redescription separates his *S. punctata* from *S. pulchra*. *S. punctata* is also similar to *S. breviseta* as redescribed here: the two species were found sympatrically in both the Swansea Bay and Northumberland material. Cuticle pattern, male amphid size and relative development of the supplements are the three most conspicuously different characters but, on the basis of the specimens available for study here, there appear to be minor differences in a number of others: compared with *S. breviseta, S. punctata* specimens have relatively slightly longer R3 sensilla (0·4 h.d. vs 0·3 h.d.), slightly less curved and shorter spicules (1·3 a.b.d. vs 1·5–1·6 a.b.d. as arc), less conspicuous median piece, slimmer tail and a different orientation of the ovaries to the gut (based only on one female *S. punctata*).

As *S. punctata* is now understood, the specimens described by Allgen (1935) and Stekhoven (1935) fit into the species (as pointed out by Jensen, 1979) but those of Timm (1952) from Maryland, U.S.A. clearly do not, since the cuticle has 'fine uniform punctation'.

Sabatieria longispinosa Lorenzen, 1972
Figs 14–15

MATERIAL STUDIED. 2♂♂ from Strangford Lough, N Ireland; slides BM(NH) 1982.7.76–77. 2♀♀ from South Bay, N Ireland; slide BM(NH) 1982.7.78. 3♂♂, 1♀, 2 juveniles from the Øresund; slides BM(NH) 1982.7.79–81. Strangford Lough: intertidal sandflat 3–5 cm depth, Station C (see Platt, 1977). South Bay: intertidal sand, 1–12 cm depth (see Boaden & Platt, 1971). Øresund: 15–16 m subtidal fine sand, 7–15 cm (collected by Dr P. Jensen, March 1978 and March 1979).

MEASUREMENTS (in μm) AND DEMANIAN RATIOS (of specimens from Strangford Lough, Northern Ireland only).
Males (♂1, ♂2 respectively). Total body length: 2440; 2495. Demanian ratio a: 104; 109. Demanian ratio b: 14·6; 14·9. Demanian ratio c: 26·0; 25·7. R3 sensilla length: 26; 26. Head diameter: 10; 11. Oesophagus length: 167; 168. Posterior oesophagus c.d.: 19; 20. Maximum body diameter: 22; 23. Spicule length (chord): 27; 26. Anal body diameter: 20; 21. Cloaca to anterior supplement (β): 83; 85. Tail length: 94; 97.
Females (♀1, ♀2 respectively). Total body length: 2650; 2790. Demanian ratio a: 98: 93. Demanian ratio b: 14·0; 16·0. Demanian ratio c: 23·5; 26·8. R3 sensilla length: 25; 23. Head diameter: 11·5; 11. Amphid diameter: 7: 7; Amphid c.d.: 12; 10. Oesophagus length: 189; 174. Posterior oesophagus c.d.: 27; 27. Maximum body diameter: 27; 30. Anal body diameter: 23; 23. Tail length: 113; 104. Vulva to anterior: 1585; 1580.

DESCRIPTION. The following morphometric data is based on the Irish specimens, unless stated otherwise. Elongated body. Cuticle annulated and finely punctated. Punctations may be difficult to detect mid-body: most distinct in anterior oesophagus and tail regions. Dots are slightly larger laterally than sublaterally, but are all more or less organised into transverse

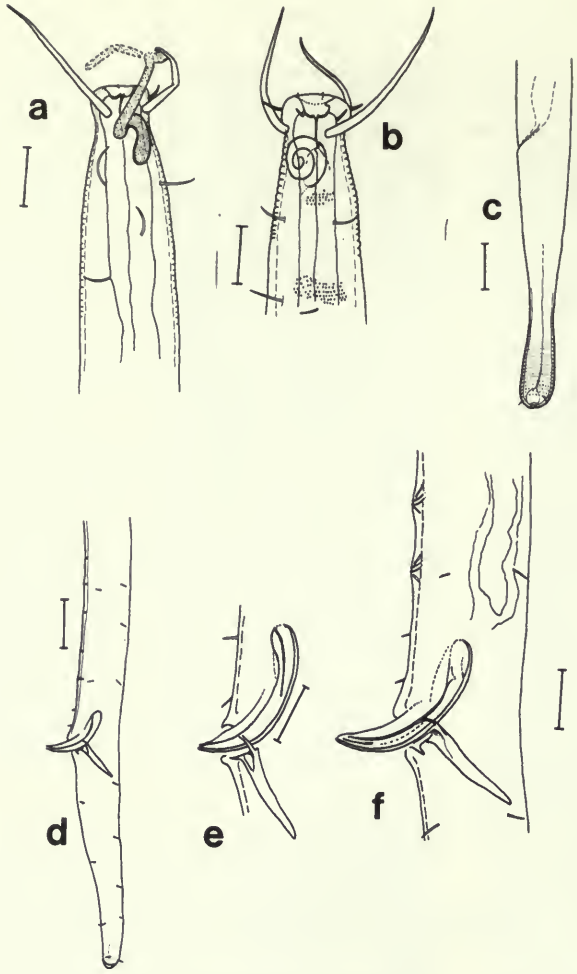

Fig. 14 *Sabatieria longispinosa* from Strangford Lough: (a) ♂1 head; (b) ♀1 head; (c) ♀1 tail; (d) ♂1 posterior region; (e) ♂2 copulatory apparatus; (f) ♂1 copulatory apparatus. Bar scales: c, d = 20 μm; others = 10 μm.

rows. There are fewer rows laterally than sublaterally in the anterior part of the oesophagus; for example, in one of the males from the Øresund, just posterior to the amphid there are 7 lateral rows per 10 μm and 14 dorso-sublateral rows per 10 μm. In one of the males from Strangford Lough, in the lateral field there are, per 10 μm, 9 rows immediately posterior to the amphids, 20 rows mid-body and 13 rows in the anterior part of the tail. The punctation is particularly noticeable on the tail-tip of females (Fig. 14c). In males from the Øresund, quite conspicuous sublateral cuticle pores were observed in the cervical and caudal regions (Fig. 15d). Two sublateral pairs of 6–8 μm cervical setae are situated about 2 and 3 h.d. from anterior, followed by sublateral files of shorter somatic setae. R1 sensilla papilliform. R2 sensilla 2–3 μm, setiform. R3 sensilla 26 μm in males (2·4–2·6 h.d.) and 23–25 μm in females (2·1–2·2 h.d.). In the male specimens studied here, the corpus gelatum was displaced so that the exact dimensions or number of turns could not be determined. However, a male described by Riemann (1966) from the Elbe estuary had $3\frac{1}{4}$ turns and was just over 90% c.d. The amphids of Irish females are 7 μm wide, 60–70% c.d. with almost $2\frac{1}{2}$ turns. Excretory pore at 70–75% of oesophagus length. Tail 4·5–5 a.b.d. but there is sexual dimorphism in the shape: females have a much more conspicuously swollen tip (Fig. 14c).

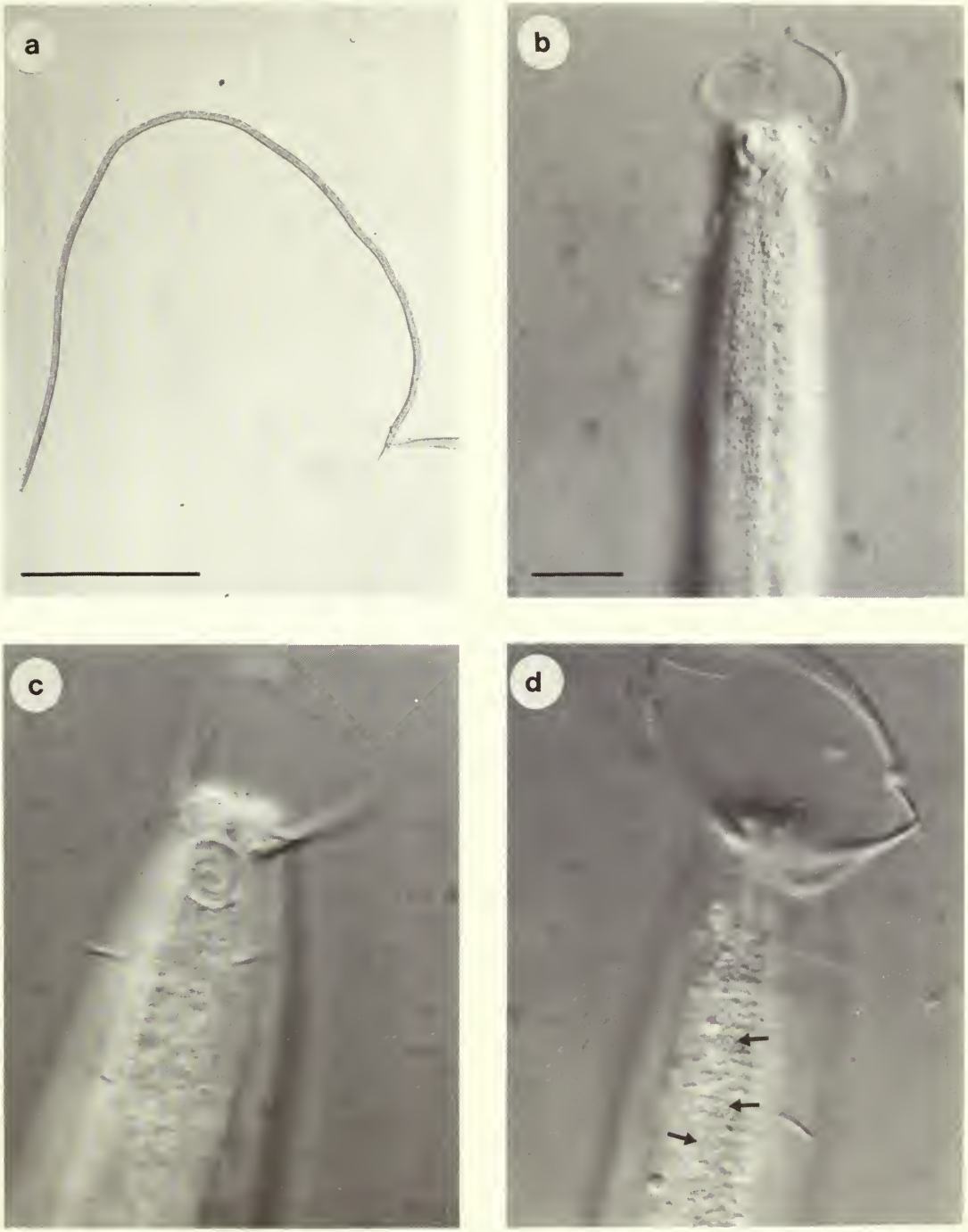

Fig. 15 *Sabatieria longispinosa* from Strangford Lough (a–c) and the Øresund: (a) entire ♂; (b) ♂ anterior showing cuticle pattern; (c) ♀ head; (d) ♂ head showing cuticle pores, some arrowed. Bar scales: a = 500 μm; for others, as in b = 10 μm.

Spicules equal, curved; 1·2–1·4 a.b.d. (chord). Gubernaculum with paired apophyses, 17–19 μm long (60–70% of spicule chord length). Two ventral precloacal spines, 8–10 μm and 18–19 μm from cloaca. Five more or less equally spaced tubular precloacal supplements, 11–17 μm apart: anteriormost 83–85 μm (β) from cloaca, 3·4% of total body length. Two opposed testes: anterior left, posterior right of gut.

Ovaries opposed, outstretched: anterior left, posterior right of gut. V = 57–60%. Eggs elongated.

REMARKS. The females described here were originally reported as *S. armata* Gerlach, 1952 (Boaden & Platt, 1971). However, *S. armata* females have more slender tails (6·2–7·3 a.b.d.) and the males have 9 precloacal supplements (anteriormost 4·9% of total body length from

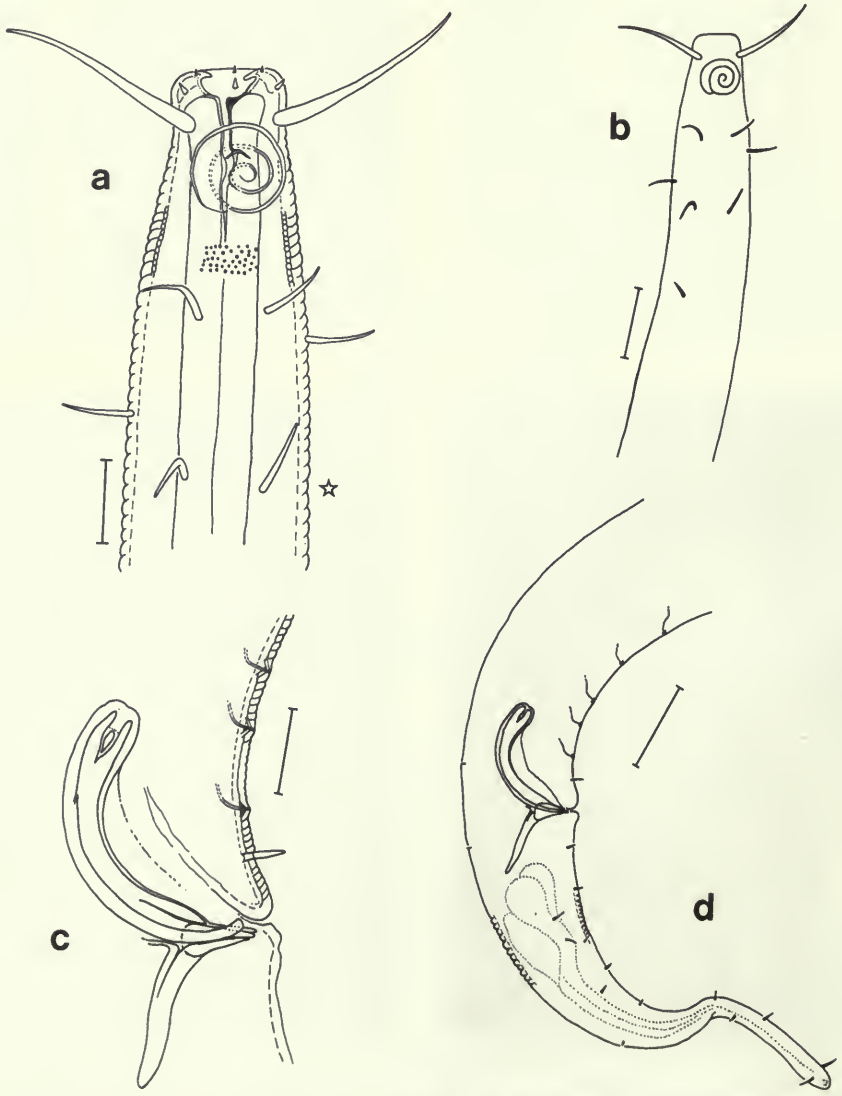

Fig. 16 *Sabatieria elongata* from Firth of Clyde: (a) ♂1 head with part of amphid shown hatched to avoid obscuring buccal cavity and star indicating ventral side; (b) ♂1 anterior region to show disposition of cervical setae; (c) ♂1 copulatory apparatus; (d) ♂1 posterior region. Bar scales: d = 25 μm; b = 20 μm; a, c = 10 μm.

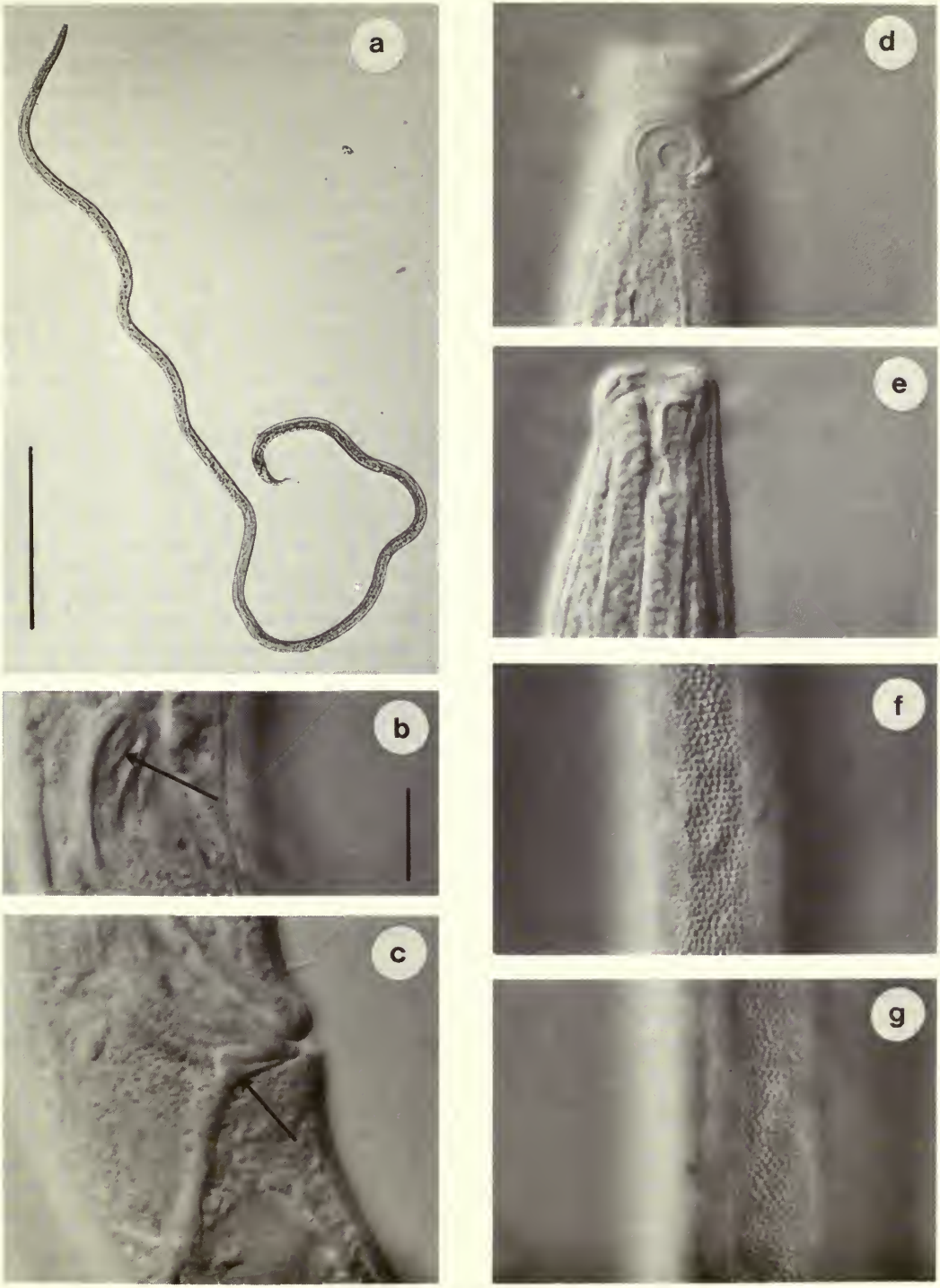

Fig. 17 *Sabatieria elongata* from Firth of Clyde: (a) entire ♂; (b) proximal part of spicule showing median list (arrow); (c) cloacal region showing triangular guiding piece (arrow); (d) anterior region showing amphid; (e) anterior region showing buccal cavity; (f) lateral cuticle in anterior oesophagus region; (g) lateral cuticle in mid-body region. Bar scales: a = 500 μm; for others, as in b = 10 μm.

cloaca). The specimens are identical to *S. longispinosa,* as redescribed by Riemann (1966). My attention was drawn to the cuticle pores and the conspicuous punctation on the tip of the female tail by Dr P. Jensen (pers. comm.): these features had not hitherto been reported.

Sabatieria elongata Jayasree & Warwick, 1977
Figs 16–17

MATERIAL STUDIED. Lectotype ♂1 (being the ♂1 of Jayasree & Warwick, 1977: their Fig. 6a–c) and paralectotype ♂2, both on slide BM(NH) 1975.1184. Low water, Irvine Bay, Firth of Clyde, Scotland. Collected by Dr K. Jayasree, August 1974.

MEASUREMENTS (from Jayasree & Warwick, 1977)

♂1: $\frac{-\ 220\ M\ 3433}{15\quad 32\quad 39\quad 34}$ 3575 µm; a=92; b=16·3; c=25·2; S=31 µm

♂2: $\frac{-\ 225\ M\ 3280}{15\quad 31\quad 38\quad 34}$ 3430 µm; a=90; b=15·3; c=22·9; S=31 µm

DESCRIPTION. The following information is supplementary or additional to the original description. Cuticle annulated, most noticeably in the anterior oesophagus and caudal regions, and punctated. The punctation is arranged more or less in transverse rows; but there are fewer rows of larger dots in the lateral field, beginning immediately posterior to the amphids, and they tend to be more irregularly arranged. The lateral dots are most noticeably larger in the anterior oesophagus region and the conical part of the tail. Just posterior to the oesophagus, there are 13–14 rows of punctations per 10 µm in the lateral field but 20–21 rows medial to this. In both specimens, there was a similar bilateral arrangement of long cervical setae (Fig. 16b): sublateral pairs at 25–30 µm and 47–51 µm from the anterior with submedian pairs between them, followed by a single dorso-sublateral. Short but sparse sublateral somatic setae are present throughout the body posterior to the cervical setae, with extra subventral setae on the male tail. The ventral section of the cup-shaped part of the buccal cavity is more heavily cuticularised than the dorsal section, and at one depth of focus resembles a tooth (Fig. 16a). The tubular, non-expanded posterior part of the buccal cavity has a weak cuticularised projection at its base. Amphid describes 3 turns.

The distal end of the copulatory apparatus is not easy to analyse, but the spicule tips appear to be double and the gubernaculum has a solid central triangular guiding-piece (Fig. 17c). A feint ventral ala can be detected beginning near the proximal end but it could not be followed to its termination. The proximal end of the spicule has a conspicuous short median list (Fig. 17b). The lectotype male has 15 tubular precloacal supplements each terminating in a small cone. In the two specimens available, the posterior three supplements are somewhat more closely spaced: the posteriormost 5 supplements are spaced 10+7+14+14 µm apart in ♂1 and 13+15+21+18 µm apart in ♂2. In ♂1 the anterior supplement is situated 290 µm anterior to the cloaca (β); 8% of the total body length. Testes: anterior left, posterior right of gut.

REMARKS. ♂1 is here chosen from the original syntype series as the lectotype: it is in good condition, was the original figured specimen and has 15 supplements, the mid-point of the range of 13–17 quoted by Jayasree & Warwick (1977). The only points of difference compared with the original description are: 1. conspicuous lateral differentiation is present; 2. somatic setae are present throughout the body; 3. the undulating spicule alae are here interpreted as being the ventral cloacal wall.

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